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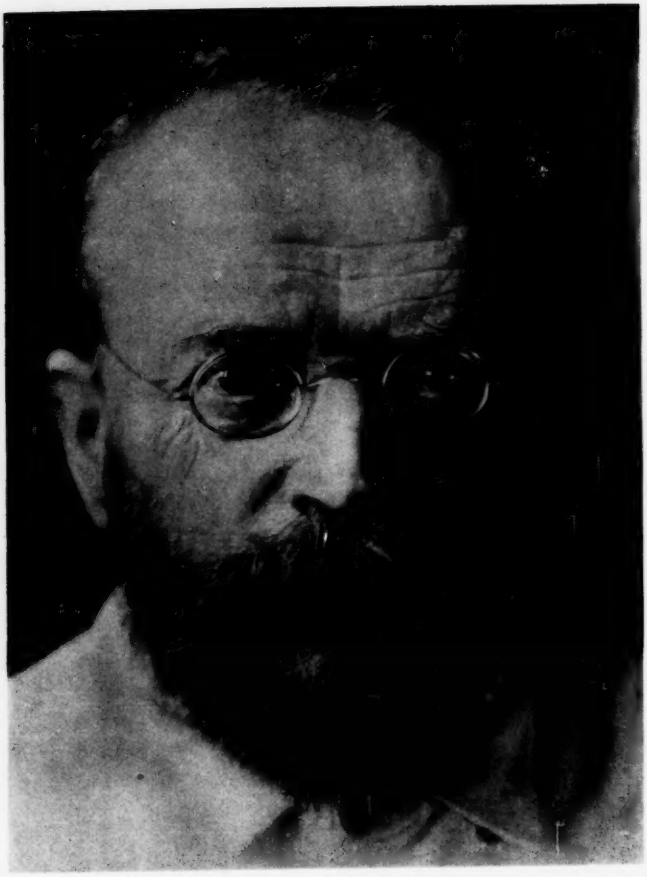

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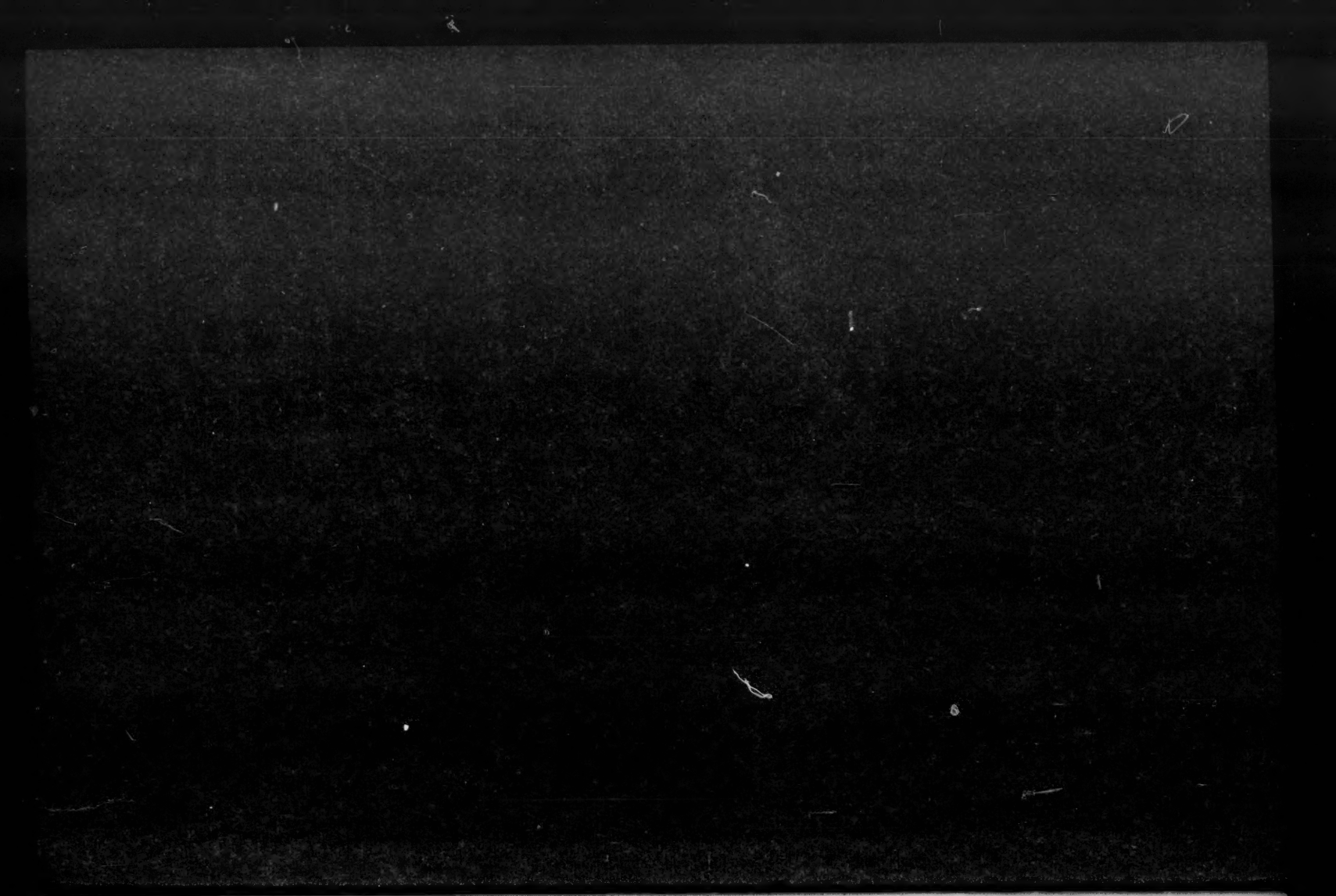

STUDIES IN FERTILITY AND INBREEDING IN SOME HERBAGE GRASSES

BY *FREDRIK NILSSON*
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I. INTRODUCTION.

THE investigations, the results of which will be given in this paper, were carried out in connection with practical grass breeding at Weibullsholm during the years 1926—1931. In the autumn of 1925 Dr. K. B. KRISTOFFERSON took charge of herbage plant breeding at Weibullsholm, and the present writer, in his capacity as assistant, was in the position to participate in the breeding work from the very beginning and to discuss with Dr. KRISTOFFERSON the problems involved in attaining practically valuable results in the work of plant breeding. Ever since 1927 the present writer was in charge of herbage plant breeding and continued the work right up to the autumn of 1931. In the work of practical grass breeding all the economically valuable species were gradually brought under cultivation.

In connection with this work there arose of course the question as to what methods could and should be employed, and it soon became evident that for the time being it would be necessary to proceed along the lines of the breeding methods adopted up to that time. Of these methods only two need be mentioned, viz. the principle of family breeding, practised in root-crops and rye, and the isolation method elaborated by WITTE (1911) for perennial grass species. The breeding of grasses carried on previously at Weibullsholm by Dr. B. KAJANUS had on the whole been in accordance with WITTE's method. The application of WITTE's method, however, requires a knowledge of the self-fertilizing capacity of the various species of grasses and the effect of inbreeding upon the progeny.

For the purpose of studying these conditions more closely investigations were started on seed-setting in isolation and the development of the progeny after self-fertilization. These investigations were commenced in 1926 and were continued up to the autumn of 1931. Starting with *Festuca pratensis*, *Dactylis glomerata* and *Phleum pratense* the investigations were extended so as to include the *Lolium* species, *Festuca rubra*, *Poa pratensis* and *Alopecurus pratensis*. When these investiga-

tions were started other researchers in different countries had contributed to our knowledge of the problems involved, chiefly relating to the tall hay-grasses (FRANDSEN 1917, FRUWIRTH 1916, 1920, 1924, HAYES and BARKER 1922, HAYES and CLARKE 1925, JENKIN 1924, KNUTH 1898, MC ROSTIE 1925, RAUM 1914, WEBBER 1912, WITTE 1915, 1919 a—c, 1922). Since then a number of publications have appeared, which throw further light on these questions (CLARKE 1927, KNOLL 1929, JENKIN 1928, 1930, 1931 a—d, STAPLEDON 1931, TROLL 1931, SYLVÉN 1929, VALLE 1931 b, BEDDOWS 1931), in addition to which data have been published with regard to the fertility and inbreeding of pasture grasses (JENKIN 1931 d, TROLL 1931, VALLE 1931 a, NILSSON-LEISSNER 1933).

The present investigations are not to be regarded as concluded and the writer would have preferred to continue them for another year or two before publishing. On his departure from Weibullsholm in the autumn of 1931, however, he had to leave the material behind, and as there is no longer any possibility of continuing the investigations on the material the writer has deemed it advisable to publish the results attained and in conjunction therewith to discuss the conclusions that may be drawn and their application to practical breeding methods.

Before proceeding to give an account of the results obtained and how they were achieved I wish to express my indebtedness to Professor H. NILSSON-EHLE, Svalöf, for the interest he has shown in the investigations and for his readiness to grant working facilities during the time I have been employed at Sveriges Utsädesförening. I also wish to tender special thanks to Dr. K. B. KRISTOFFERSON, Härnösand, for valuable suggestions during the years 1926—1927, and to Dr. O. TEDIN, Svalöf, for the interest he has shown in the work and for his valuable comments and advice on working the material, especially the mathematical treatment. I also received his assistance in setting up formula (6) mentioned below. Further, I wish to tender my most sincere thanks to Dr. R. A. FISHER, Rothamsted, and to Mr. J. W. HOPKINS at the same station for furnishing the mathematical proofs to formulae (7) and (8). My colleagues at Svalöf, Dr. N. SYLVÉN and Dr. G. NILSSON-LEISSNER, as well as Dr. G. TURESSON, Lund, I gratefully thank for the interest they have shown in my work and for advice given during its progress.

In conclusion I wish to mention that I have received valuable assistance from my wife, Mrs. MARTHA NILSSON, as well as from Miss INGA PALM in the technical operations of measuring and determining the seed setting.

PROBLEMS.

The problems that had to be solved, or at any rate brought nearer solution, were the following:

1) Determination of the self-fertility of the economically important species of grasses, especially the amount of seed-setting in enforced self-fertilization.

2) To find out if different degrees of self-fertility occur in different strains and biotypes within the same species.

3) The relation between self-fertility and general fertility in open pollination.

4) The heredity of self-fertility.

5) The effect of self-fertilization on the development of the progeny, and

6) Testing if the results were in agreement with current theories of inbreeding.

Part of the results obtained has already been published. Thus, a report has been given of the *Lolium* species (F. NILSSON 1930, 1933 b) and of *Festuca rubra, Poa pratensis* and *Alopecurus pratensis* (F. NILSSON 1933 a). This paper will therefore mainly comprise data concerning *Festuca pratensis, Dactylis glomerata* and *Phleum pratense.* A brief survey of the previously published results in other species will be added, together with a discussion of the results in the species investigated.

In the following account a survey will first be given of the material employed and the methods applied, both technically and mathematically, after which the results obtained will be given for each species separately. The principle adopted is first to give an account of the tests of fertility and then of the effect of inbreeding on the progeny. A retrospective survey will be given of the results of the investigations on each species and finally a discussion of the results in comparison with those of other researchers in the same field.

II. MATERIAL AND METHODS.

1. MATERIAL.

The material employed in these investigations was taken chiefly from commercial strains and from selected strains existent at Weibullsholm when the investigations were started. All plants isolated in 1926 and 1927 were selected because of their desirable appearance in different characters with the intention of obtaining strains uniform as regards

practically valuable characters. Concerning timothy plants isolated in 1929 and 1930 information is given together with the accounts of the results.

a) FESTUCA PRATENSIS HUDS., MEADOW FESCUE.

In the spring of 1925 Mr. S. O. BERG had raised plant material for practical selection in the following strains: *Weibull's selected* strain, *Weibull's Mimer*, *Dœhnfeldt's* strain, *Svalöf's early* and *Svalöf's late* strain. Of these strains at least 200 plants were planted with a distance of 30 × 40 cm. between each plant. These populations, which form the basic material of the meadow fescue investigations, were well developed and vigorous, but they exhibited very great variation in a number of characters. This high degree of variation indicated that each population was composed of a great many types, from which there was every prospect of differentiating, by means of selection, a number of more or less valuable biotypes. The strains, all of which are products of selection, thus proved to be by no means uniform when single individuals were spaced. None of them could be considered entirely free from previous inbreeding but all seem to have been produced by a more or less rigorous inbreeding, which cannot, however, have been carried on for more than one generation. *Svalöf's* strains had been raised in accordance with WITTE's breeding method from isolated clones of wild plants, while *Weibull's Mimer* is derived from a plant of *Weibull's selected* strain (BERG 1927). No accurate records of derivation are found for the latter strain and *Dœhnfeldt's* strain. Owing to the lack of complete information concerning previous inbreeding all strains are designated I_0, making allowance for the possible inbreeding in one generation, the effect of which may be assumed to have been annulled by several generations of commercial seed growing. Of these strains 158 plants in all were isolated in 1926 and when the isolations were harvested seeds were also collected after free flowering. In connection with some crossing experiments in 1928 three plants were isolated in a greenhouse and eight plants in the open field.

b) DACTYLIS GLOMERATA L., COCKSFOOT.

In 1926 there was at the station a cocksfoot population of about 200 plants of each of the strains *Svalöf's Skandia*, *Weibull's Minerva II*, *Weibull's Tardus*, and the new strains, *413* and *453*, which had been raised at Weibullsholm but had not been put on the market. Each of these strains, which form the basic material of the investigations on

cocksfoot grass, exhibited great variability between the different individuals and they offered the possibility of breeding different types. None of them is entirely free from past inbreeding and according to available records they can be referred to different generations of inbreeding. *Skandia* (WITTE 1914) and *Tardus* (KAJANUS 1920) are derived from two different mother plants of wild Swedish cocksfoot, and in this paper they are designated, like the meadow fescue strains, as I_0, while the other strains receive the designation I_1, as they demonstrably belong to a later generation of inbreeding than *Skandia* and *Tardus*. *Minerva II* is derived from an isolated plant of *Skandia* (BERG 1926), *413* in the same manner from *Tardus* and *453* from another unnamed strain. When these investigations were started the supply of *Minerva II*, *413* and *453* consisted of seedlings from families, separated in isolation islands for one generation, these families again being derived from individual plants isolated in pergamine bags. Hence these strains may be regarded as I_1-generations, whereas *Skandia* and *Tardus*, although derived from individual plants, can no longer be considered to belong to any definite inbreeding generation as they have been propagated for several generations on a large scale. Of the strains mentioned above 229 plants in all were isolated in 1926, from which seed was also harvested after free flowering.

c) PHLEUM PRATENSE L., TIMOTHY.

The timothy material also consists mainly of commercial strains, spaced plants of which were available already in 1926 or raised later on from samples of seeds procured. In 1926 isolations were performed on altogether 60 plants from the strains *Weibull's Kämpe*, *Svalöf's Gloria*, *No. 121* and Swedish *Common commercial* timothy. At the same time seeds were collected and sown from a number of isolations carried out in 1925 by Mr. S. O. BERG on the strains *121* and *404*. In 1927 there were also added *Svalöf's Primus*, *Weibull's Freja*, *Finnish timothy*, *Russian timothy* and strain *No. 397* raised at Weibullsholm. All these strains belong to the erect, tall type of timothy, to which JENKIN (1931 d) has given the names »hay-type» and »semi-hay type», and should be referred to the type classified by GREGOR and SANSOME (1930) as Group I with a somatic chromosome number of 42. The strains have been subjected to previous inbreeding to a varying extent. Nothing is known of the *Russian timothy* in this respect, as it had been raised from a seed-sample obtained through the Russian Commercial Delegation at Stockholm. *Kämpe* and *Freja* (W. Weibulls Årsbok 1922)

as well as *Primus* (WITTE 1916) and *Gloria* (WITTE 1920) are strains bred in accordance with WITTE's breeding method. *Kämpe* is derived from *Finnish timothy*, while the other strains trace their origin from wild-growing Swedish timothy plants. Of the other strains the one designated *Finnish timothy* was a direct second generation of a Finnish commercial sample, *404* a second inbreeding generation derived from *Kämpe*, while *121* and *397* represent direct products of self-fertilization in one generation of wild Swedish timothy plants. In the following report *Finnish timothy* and strain *No. 404* are designated I_2 and strains *Nos. 121* and *397* as I_1. All the others are designated I_0, allowing for the inbreeding of one generation in the breeding of the strains, in conformity with what was said above regarding meadow fescue and cocksfoot.

In addition to the strains mentioned above isolations were made in 1930 on 14 transplanted wild timothy plants, 5 of which belonged to *Phleum pratense* var. *nodosum* L. from the island of Öland, and 10 plants, also of the *nodosum* type, derived from seeds produced by a Russian seed-sample obtained in 1928. These plants, which correspond to JENKIN's »pasture type», should probably be referred to GREGOR and SANSOME's Group II with a somatic chromosome number of 14.

2. EXPERIMENTAL METHODS.

Accurate counts of fertility have been performed in *Festuca pratensis* and *Phleum pratense*, whereas the results in *Dactylis glomerata* are based only on observations. The species subjected to the most thorough examination is *Phleum pratense*, in which it was possible to follow the »self-fertility» from mother plants to progeny. The investigations into the effect of self-fertilization on the progeny are based, partly on general observations of the development and the appearance of various characters and partly on accurate measurements of the variability. As I was not in a position to determine the vigour in the separate individuals by means of weighing, as was done by JENKIN (1926) and VALLE (1931 a and b) in their researches on inbreeding effect in *Lolium perenne*, *Phleum pratense* and *Festuca rubra*, I considered it most appropriate that a close study should be made of some definite character and thus the height was chosen as being an easily measurable character, which had also been closely studied in previous inbreeding investigations on different species (SHULL, EAST, JONES, HERIBERT NILSSON, VALLE and others). An analysis has been made of the variation in height in the material in its entirety but even other characters, especially in some

families of timothy, have been analysed, such as length of panicle and tillering.

In meadow fescue it has only been possible to examine one inbreeding generation, and this was also the case in cocksfoot grass, where different strains, as has already been discussed, represent different inbreeding generations owing to earlier inbreeding. The investigations in timothy comprise different generations from the first to the fourth inbreeding generation, but it should be noted, however, that there are no comparisons between all the generations. The extensive timothy material is treated according to the different years during which the mother plants were selected.

a) FERTILITY.

All the isolations, except a few plants of meadow fescue which will be dealt with below, were performed in the open. The isolating material employed consisted of double pergamine bags of rather large dimensions. The technique of isolation was only varied in one detail, that is, in tying the bags. Besides the usual method of tying the bags at the top and bottom trials were made in 1926, on the suggestion of Dr. K. B. KRISTOFFERSON, to hold the upper part of the bag loosely by means of a ring fixed to the top of the bag. This resulted, however, only in the enclosed panicles being more easily damaged and having to be rejected at harvest.

In all isolations as far as possible 3 panicles in the same stage of development and on about equally tall straws were enclosed in each bag and 2 parallel isolations were made on each plant. In 1927, however, 4 parallel isolations were made on each plant. When harvested all the isolations were examined very carefully and whenever the bag was found damaged the isolation was rejected. The isolating bags were left untouched until the panicles were threshed and in harvesting the seeds the isolated panicles were cut off from their plants. After free flowering at least 3 large and normally developed panicles were harvested in order to examine the seed-setting.

It has not been possible to examine exactly the seed-setting in all the isolated material, in a number of cases it has only been graded after threshing and records kept of the number of seedlings after the sowing of the seeds. In the meadow fescue plants isolated in 1928 the seed-setting was, however, accurately determined by counting the number of flowers and seeds produced. The seed-setting in timothy was

determined in the same manner as in earlier investigations (WITTE, SYLVÉN, VALLE and others), by counting the number of seeds per panicle and measuring the length of the panicle, by means of which the seed-setting per cm. of the panicle length could be calculated. In a number of the 1927 isolations, however, only the number of seeds per panicle was determined.

b) INBREEDING EFFECTS.

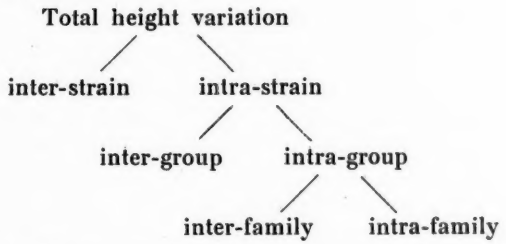
In order to estimate the development of the progeny after self-fertilization seedlings were raised also from seeds after free flowering for the sake of comparison, and in addition the isolated mother plants were preserved and after vegetative increase were planted beside their progeny. The mother plants in the cocksfoot and meadow fescue material and in the timothy material isolated in 1926 and 1927 were, however, planted out too late in the autumn of 1928, hence they did not reach that degree of development required for a direct comparison with the progeny. When seedlings after the 1929 harvest were being planted in the summer of 1930 ten evenly sized cuttings of the mother plants were also planted out at the same time so as to obtain as equal a degree of development as possible for the next year. In the investigations performed in 1931 comparisons could also be made between mother plants and their progenies. For the rest, the investigations on inbreeding were based on comparisons between families after isolation and open pollination derived from the same mother plant. The seedlings were obtained from seeds sown in sterilized earth in pots, and after transplantation the plants were planted in the open with a distance of 30×40 cm. between each plant. Families obtained after isolation and after free flowering from the same mother plant were placed side by side in order to ensure the best possible material for comparison. The designation of the material is the same as that applied by VALLE (1931 b) to his timothy material. Families after isolation are designated I_1, I_2, I_3 according to the inbreeding generation to which they belong, and families after free flowering are designated K. Thus, the designation I_2K denotes a family derived from an open pollinated I_2 plant.

By inbreeding effect is meant, unless otherwise stated, as in the timothy investigations of 1931, the differences that can be observed to occur in the various characters between families after isolation and free flowering. As already mentioned (page 6), the height of the plants especially has been studied very carefully in the different families as well as the variability occurring in this character. As it occurs very

often that individual panicles are excessive the principle adopted in measuring the height was to take the second highest panicle as the highest point. Thus, by height is meant the distance from the surface of the ground to the summit of the next tallest stem, measured vertically. The measurements were carried out during the flowering stage and are true to 1 cm. Other characters examined are the length of the panicles and the tillering. The length of the isolated panicles in timothy was measured. Measurements were also made on all plants in a number of families, when the length of the panicles of the three tallest straws on each plant was determined. The tillering in timothy was determined in some highly variable families by measuring the circumference of the plant 10 cm. above the surface of the ground. In these cases the straws were uniformly pressed together before the measurements were taken. Data relating to other characters have also been collected, particulars of which will be given for each group of the material separately.

3. MATHEMATICAL METHODS.

The numerical material obtained in these investigations has been treated mathematically in accordance with the methods of analysis developed by FISHER (1930). As no detailed references will be given in this report when dealing with the separate cases it may be necessary to give a somewhat comprehensive explanation of the procedure in the mathematical operations and the testing of the statistical data. In the analysis of variance of separate characters, such as fertility, height, length of panicle, etc., the same method is employed and by way of example the procedure in the analysis of height may be given. In order to illustrate the possible grouping of the aggregate variation in height in the entire material determined during one year the following schematic survey is given:



The families are of two kinds, viz. *I* and *K* families, which have been arranged into groups, each consisting of one *I* family and one *K* family

derived from the same mother plant. By adding all groups belonging to the same strain we get the total variation within each strain and by adding together all the strains we obtain the total variation. This was also the method employed in the calculations performed, beginning with the separate families which were successively coordinated into groups and strains. Special combinations were also made, as for instance, of all *I* families and of all *K* families, thus procuring a comparison between the entire *I* material and the entire *K* material, first within each strain and then within the material as a whole.

The height variation within the separate families is determined with the aid of the mean and the deviations from it by the usual formula

$$\sigma^2 = \frac{\Sigma d^2}{n-1} \tag{1}$$

With an *I* family and its corresponding *K* family, having n_1 and n_2 individuals respectively, a group is formed, the total variation of which is found by the formula:

$$\sigma_t^2 = \frac{\Sigma \delta^2}{n_1 + n_2 - 1} \tag{2}$$

This total variation within the group can, however, also be found by summing the sums of squares and D. F. (degrees of freedom) from the intra-family and inter-family variation within the group. These are computed by the formulae:

$$\text{intraclass variance } (\text{var}_{ab}) = \frac{\Sigma d_1^{\,2} + \Sigma d_2^{\,2}}{n_1 + n_2 - 2} \tag{3}$$

$$\text{interclass variance } (\text{var}_p) = \frac{\Sigma(nD^2)}{2-1} \tag{4}$$

In formulae (2)—(4) δ is equal to the deviation of the individual variants from the group mean, d_1 and d_2 are the individual deviations in the respective families from the family mean, D is the difference of the family mean from the group mean. Formulae (3) and (4) are extensively used in determining the intraclass and interclass variance and are also applied for finding the intra- and inter-group variation, intra- and inter-strain variation, etc.

Thus, for instance, the total intra-group variation within each

strain is obtained by summation of the sum of squares and D. F. for each group and the inter-group variation by the formula:

$$\text{Inter-group variance} = \frac{\Sigma\{(n_1 + n_2)\triangle^2\}}{g - 1} \tag{5}$$

which is only an application of formula (4) with g = number of the groups and $\triangle$ = the deviation of the group means from the total mean.

In comparing the variances in different families, groups or series, etc. FISHER's (l. c.) z is employed to determine the statistical significance, FISHER's Table VI being a valuable aid to determine quickly what values of z should be reached in a certain number of D. F.'s so that there is sufficient probability for differences not attained by chance variation alone. As limitation value the 5 per cent. point of z was employed, which corresponds to a probability of 95 : 5 that a certain value is not obtained by chance variation alone. In this report a difference is considered to be significant if z reaches a value that is at least equal to the 0,05 point in chance variation.

The inbreeding effect in height after different mother plants is determined by the difference of the mean heights in the *K* and *I* families (in the 1931 timothy material also by the difference between mother clone and progeny) and is given in absolute figures. The average inbreeding effect is determined for each strain by weighting the effect in the individual groups with the »*effective n*», which is found for each group by the formula:

$$\textit{Eff. } n = \frac{n_1 \cdot n_2}{n_1 + n_2} \tag{6}$$

The analysis of variance of the inbreeding effect in each strain is calculated by means of the following formulae:

$$\text{Intraclass variance} = \frac{\Sigma\{\Sigma d_1^2 + \Sigma d_2^2\}}{\Sigma(n_1 + n_2 - 2)} \tag{7}$$

$$\text{Interclass variance} = \frac{\Sigma\left\{\frac{n_1 \cdot n_2}{n_1 + n_2} \cdot \xi\right\}}{g - 1} \tag{8}$$

In these formulae, n_1 and n_2 denote, as previously, the number of individuals in the respective *I* and *K* families within each group, g is

the number of groups within the strain and ξ the difference between the inbreeding effect of the individual group and the mean effect of the strain. The total intraclass variance is determined for all strains within a species by summation of the sum of squares and the D. F. for the total variance of each strain, and the interclass variance is obtained by the usual formula for interclass variance (4), applying $\Sigma\left\{\frac{n_1 \cdot n_2}{n_1 + n_2}\right\}$ for each strain.

The following derivation of formula (6) may be furnished: The principle of the analysis of variance is the weighting of each class-deviation from the total mean against the variance of the class-mean. The variance of the class-mean is obtained by the formula v/n, where v is the variance within the class, n the number of individuals in the class. The smaller the variance of the mean, the greater the weight of its difference from the total mean, and the weighting is made by multiplying the d^2-value of the class with the inverse value of the variance of the class-mean, *i. e.* with n/v. When v is supposed to be the same in all classes, the weighting is thus made simply by multiplying each class-d^2 by the n of the class. The fact may also be stated in the following words: in determining the Σd^2 for the interclass-variance, each class-d^2 should be multiplied with the same value, which is used as denominator in determining the variance of the class-mean. Now, when we want to determine the variance of a difference between the means of two sets of observations, we have to use the formula $v_1/n_1 + v_2/n_2$. If here again $v_1 = v_2$, we have $v/n_1 + v/n_2 = \frac{v}{\frac{n_1 \cdot n_2}{n_1 + n_2}}$. In calculating the variance of the difference we have, thus, to use the denominator $n_1 n_2/(n_1 + n_2)$. Finally, in determining the interclass variance of a series of such differences, we should multiply the square of the difference between each individual difference and the mean of all with this denominator. This value has in this paper been termed »*the effective n*».

In determining the correlation between the variations in different series the coefficients of correlation and regression were calculated by the formulae:

$$r = \frac{\Sigma(d_x \cdot d_y)}{n \cdot \sigma_x \cdot \sigma_y} \tag{9}$$

$$R = \frac{\Sigma(d_x \cdot d_y)}{\Sigma d_x^2} \tag{10}$$

These formulae, however, have a limited application, as they are only reliable when single observations in both the series are put together. If the variants of one or both of the variation series are made up of means from a number of observations then weighting must be made with the number of observations within each pair, thus the

numerator will be $\Sigma\ (n_p . d_x . d_y)$. By the formula for interclass variance (4) the sum of squares will also be greater, hence the formula for the coefficient of regression will have the following appearance:

$$R = \frac{\Sigma(n_p . d_x . d_y)}{\Sigma(n_p . d_x^2)} \qquad (11)$$

This application of weighting has been made in all the calculations with the exception of the correlation calculations between the found inbreeding effect in height and the variance in the *I* families. In these cases there seemed no prospects of obtaining a greater reliability in the correlation in proportion to the increased labour and therefore formula (9) was applied. On the meadow fescue material, however, a comparative calculation was made by both formulae, when a very slight difference ($r = +\ 0{,}245$ and $+\ 0{,}246$) was obtained without any statistical significance. If only the *coefficients* of correlation and regression are calculated small differences in the values are obtained in other cases by the different methods, unless the number of observations varies very much.

The variation in the relative character (y) round the regression line is calculated thus: first we determine that part of the interclass variance in y, which is correlated with the interclass variance in x (the assumed character) by the formula:

$$\text{Correlated variance in } y = R\ .\ \Sigma(d_x d_y) \qquad (12)$$

after which the variance around the regression line is obtained by subtracting the value thus obtained from the total interclass variance in y.

The significance of the regression is tested by means of the analysis of variance and the use of z, as presented by FISHER (l. c.). The significance of the correlation is not tested by the standard error but by the use of z and FISHER's Tables V A and V B (l. c.). A correlation is assumed to be significant when there is a probability of at least 95 : 5 that a value obtained cannot arise merely by chance variation.

In all those cases stated in this report where the statistical significance is not given exactly, the probability is decidedly greater or less than the values given above, and for this reason it is assumed, either that there exists a significant difference in variance or a significant correlation or that there is no sufficient proof for such differences or correlations.

On some of the timothy material the skewness of the height variability has been determined in *I* as well as in *K* families. In these calculations, the results of which are given in Tables 38—41 (pp. 75—79), the methods and formulae given by FISHER, IMMER and TEDIN (1932) have been used. The height values have been grouped in 5 cm. classes taking class 0—5 as number 1, and then class numbers have been used in computing k_1, k_2, k_3 and g. Thus, if k_1- and k_2-values are to be compared with the means and variances of the same material given elsewhere k_1 must be multiplied by 5 and k_2 by 25.

III. EXPERIMENTAL RESULTS.

1. FESTUCA PRATENSIS HUDS., MEADOW FESCUE.

a) FERTILITY.

No accurate determinations were made of the seed setting in the isolations of meadow fescue carried out in 1926. The seed setting, however, varied very much in the different individuals, which was indeed observed already when the isolated panicles were threshed and again in the seedling number after sowing in 1927. Thus, some plants did not yield any progeny at all, while others proved to be relatively highly self-fertile. On the average, however, the seed setting in these isolations was low, which denotes that the degree of »self-fertility» in meadow fescue is low. Whether there are any differences between the different strains cannot at present be determined. That there are great individual differences in »self-fertility» in meadow fescue has, however, been ascertained in other material examined in 1928. In that year 3 plants of *Weibull's Mimer* were isolated in a greenhouse and 8 plants, some *Mimer* and some other strains, isolated in the open field. The results of these isolations will be seen in Tables 1 and 2. The seed setting was in both cases determined by counting the number of flowers and seeds. In the greenhouse isolations it was possible to reckon each panicle separately, as only one panicle was enclosed in each bag, but in the isolations in the open I was only able to determine the aggregate number of flowers and seeds on all the panicles enclosed in every bag. When several panicles are enclosed in one bag it is not possible at maturity to keep the panicles apart, for the seeds easily fall out and become mixed together. For comparison with self-fertility on isolation the seed setting in free flowering has been examined on 3

panicles of every plant isolated in the open. These figures are given in Table 4.

At the same time as the seed setting was being examined a measure-

TABLE 1. *Meadow Fescue Isolations in Greenhouse in 1928.*

Plant No.	Number			% Seed setting	Σd^2	D. F.	Variance	Average number of flowers per panicle
	Panicles	Flowers	Seed					
162 B	9	1164	131	11,3	85,51	8	10,69	129,3
318	12	2274	81	3,6	62,47	11	5,68	189,5
323	7	988	84	8,5	104,71	6	17,45	141,1
Total within the plants					252,69	25	10,11	
Between the plants					318,36	2	159,18	
Total					571,05	27	21,15	

ment of the size of the panicle, by counting the number of flowers on each panicle, was also procured. The size of the panicles of the plants examined is found in Tables 1, 2 and 4, from which it will be seen that

TABLE 2. *Meadow Fescue Isolations in the Open Field in 1928.*

Plant No.	Isolation I				Isolation II				Total			Average	
	Number			% Seed setting	Number			% Seed setting	Number			% Seed setting	Number of flowers per panicle
	Panicles	Flowers	Seed		Panicles	Flowers	Seed		Panicles	Flowers	Seed		
5333	3	600	16	2,7	3	687	38	5,5	6	1287	54	4,1	214,5
34	2	376	3	0,8	2	334	3	0,9	4	710	6	0,9	177,5
35	3	568	12	2,1	2	422	7	1,7	5	990	19	1,9	198,0
36	3	862	43	5,0	3	787	30	3,8	6	1649	73	4,4	274,8
37	3	405	0	0,0	3	398	0	0,0	6	803	0	0,0	133,8
38	2	218	11	5,0	2	289	14	4,8	4	507	25	4,9	126,8
39	3	605	30	5,0	—	—	—	—	3	605	30	5,0	201,7
84	3	696	5	0,7	3	846	22	2,6	12	2952	49	1,6	246,0
»	3	621	4	0,6	3	789	18	2,3					
											Average	2,4	206,6

the number of flowers on each panicle varies very much in different plants.

In order to ascertain if the differences in seed setting on isolation and size of panicle have any deeper cause and are not only due to incidental variation or modifications a complete analysis of variance

has been made. From Table 1 it will be seen that the percentage of seed setting in the greenhouse isolations varies from 3,6 to 11,3 in these plants with an aggregate mean of 7,3 %. The variation within the plants is also rather great, but not so great that sure differences cannot

TABLE 3. *Summarizing Analysis of Variance of Seed Setting and Size of Panicles in Meadow Fescue in 1928.*

	Σd^2	D. F.	Variance
Seed Setting			
Between isolations within plants	24,08	9	2,68
» » between plants	118,83	6	19,81
Total between isolations	142,91	15	9,53
Size of Panicle (Number of flowers per panicle)			
Within plants	43761,04	38	1151,61
Between »	108017,69	7	15431,10
Total	151778,73	45	3372,86

be statistically determined, for the variation between the plants is considerably greater than within the plants (Table 1), and this difference is so statistically significant as not to be due to merely chance variation. The same thing is true also of the isolations made in the open.

TABLE 4. *Seed Setting in Free Panicles of Meadow Fescue in 1928.*

Plant No.	Number			% Seed setting	Number of flowers per panicle
	Panicles	Flowers	Seed		
5333	3	374	261	69,8	124,7
5334	3	275	147	53,5	91,7
5335	3	402	290	72,1	134,0
5336	3	458	265	57,9	152,7
5337	3	452	103	22,8	150,7
5338	3	205	173	84,4	68,3
5339	3	234	120	51,3	78,0
5384	3	235	44	18,7	78,3
			Average	53,8	109,8

The mean seed setting of all isolations amounts here to 2,4 %, varying between 0 % in No. 5337 and 5 % in No. 5339. In the 7 plants, on which parallel isolations were made, the variation between the plants is considerably greater than within the plants and this difference has great statistical significance (Table 3).

The seed setting in free inflorescences is also very variable, and there are great divergencies between different plants (Table 4). The extremes of variation consist of No. 5384 with 18,7 % and 5338 with 84,1 %. However, as the seed setting of the individual panicles has not been examined it is therefore impossible on this material to determine if the variation between the plants is greater than within the plants. Instead, the correlation between seed setting in isolation and in free flowering has therefore been calculated. A positive correlation is found in which $r = + 0{,}5895$, which, owing to the small number of pairs on which the calculation is based, cannot be proved to have any great statistical significance. (The probability is about 87 : 13.)

Proceeding from this positive correlation it will now be found, with the aid of the coefficient of regression, that the variation in »self-fertility» due to variation in general fertility amounts to a value of $\sigma^2 = 55{,}51$. The remaining portion of the variability between the plants, which in addition to chance and modifications can also be caused by independent genetic variation, amounts to $\sigma^2 = 13{,}93$. The variation within the plants, which is however to be regarded as a pure environmental variation, has according to Table 3 a variance equal to 2,68, that is to say, the remaining interclass variance is greater than the intraclass variance. The difference is significant (probability 95 : 5). Although the correlation on which the division of the variation between the plants is based is uncertain, there is reason for assuming also a genetic variation in »self-fertility» between the plants, which is not correlated with general fertility.

In Tables 2 and 3 it can be seen that the variation in the size of the panicles, determined by counting the number of flowers per panicle, is greater between the different plants than within them. In this case, too, there is great statistical certainty that the difference is greater than might be expected to arise from chance. Thus, the size of the panicles on the different plants depends on the genotypical constitution and incidental and environmental variation in conjunction, the decidedly greatest part being played by the genotypical constitution.

b) THE EFFECT OF SELF-FERTILIZATION ON THE PROGENY.

In addition to the height measurements carried out in 1929, which have been thoroughly analysed, some observations have been made on the variation in other characters after self-fertilization. Thus, it happens rather often in progenies of isolated plants that chlorophyll-deficient individuals occur. A few such chlorophyll-deficient seedlings

have appeared in different families, but not in any large numbers and no fixed numerical proportions have been possible to ascertain. It should be noted, however, that besides pure albino seedlings there also occurred yellow and yellowish green, which shows that several chlorophyll factors are active. Besides one-coloured chlorophyll variants, plants with white-streaked leaves have also been observed, which were sometimes not seen until the second year, and then most distinctly during the first month of vegetation in the spring. In summer several of these plants turned quite green, hence the abnormal development of chlorophyll in these types seems to be restricted to the juvenile stage of the plant.

On the meadow fescue material great variations have been noted with respect to the development of the plants, such as, formation of tussocks, earliness, tillering and stiffness of straw, resistancy to rust, etc., which qualities seem to vary to a much greater extent in families after isolation than after free flowering. These characters have not, however, been definitely graded in the material in its entirety but have only been noted on a few plants and families that were considered valuable in the work of practical selection. This much may, however, be said, that the families after isolation have presented a picture of great differentiation in various respects. Occasional families after isolation have also shown signs of intense segregation so that different gradations of several qualities could be ascertained. This also holds good for the height, which was thoroughly analysed and a detailed account of which will be given.

Table 5 gives the number of plants in the different families and the mean height for each family, besides which the variance is given as a measurement of the variation. In order to examine the variation in families derived from the same mother plant, corresponding *I*- and *K*-families have been grouped together, for which the total mean, as well as the total variance within each group (var_t), have been calculated. This total variance has then been divided into intraclass and interclass variance, tabulated in the last two columns. Var_{ab} denotes the intraclass variance and var_p the interclass variance within each group. A close study of the Table will at once show that in general the mean height of the *I*-families is lower than that of the corresponding *K*-families. There are however two exceptions, one being in *Daehnfeldt's strain*, group No. 5, the other in the only group representing *Svalöf's late strain*. Thus, if an inbreeding effect has occurred in the majority of the cases, displaying itself in a lower average height in the

TABLE 5. *Analysis of Variance of the Height of Inbreeding Material in Meadow Fescue in 1929.*

Group No.	Field No.	Basic population	Inbreeding generation	Number of plants	Mean height cm.	Variance	Group Mean	$Var._t$	$Var._{ab}$	$Var._p$
1	3900	Weibull's selected strain	K	13	118	62,83	116	80,52	76,83	169,00
	1	» » »	I_1	13	113	90,83				
2	5	» » »	K	28	112	48,41	110	48,26	39,11	387,00
	6	» » »	I_1	11	105	14,00				
3	7	» » »	K	28	107	32,70	105	42,36	40,56	141,00
	8	» » »	I_1	29	104	48,14				
4	11	» » »	K	28	113	76,59	109	98,03	57,24	1648,00
	12	» » »	I_1	12	99	9,73				
5	21	Daehnfeldt's strain	K	28	104	29,59	104	27,19	27,90	5,00
	22	» »	I_1	5	105	16,50				
6	25	» »	K	28	98	56,15	97	57,49	56,67	92,00
	26	» »	I_1	16	95	57,60				
7	29	» »	K	29	103	59,61	100	111,79	85,86	1071,00
	30	» »	I_1	10	91	167,56				
8	31	» »	K	28	101	31,44	100	40,86	34,80	253,00
	32	» »	I_1	9	95	46,13				
9	35	» »	K	30	104	39,62	100	98,52	79,76	1055,00
	36	» »	I_1	23	95	132,68				
10	37	» »	K	30	101	21,24	100	31,81	30,59	82,00
	38	» »	I_1	13	98	53,17				
11	39	» »	K	29	111	46,82	105	131,81	83,50	2644,00
	40	» »	I_1	25	97	126,29				
12	43	» »	K	29	113	34,29	111	32,52	26,44	323,00
	44	» »	I_1	23	108	16,45				
13	45	» »	K	29	110	69,43	109	84,62	83,47	128,00
	46	» »	I_1	11	106	122,80				
14	47	» »	K	28	104	35,67	103	29,00	28,51	55,00
	48	» »	I_1	27	102	21,08				
15	86	Weibull's Mimer	K	26	103	68,24	100	79,59	57,47	920,00
	87	» »	I_1	14	93	36,77				
16	96	» »	K	29	104	51,18	100	52,14	40,90	524,00
	97	» »	I_1	15	92	20,36				
17	98	» »	K	27	104	62,08	98	107,59	66,60	1952,00
	99	» »	I_1	20	91	72,79				
18	4000	» »	K	28	107	66,96	104	115,03	93,44	892,00
	1	» »	I_1	10	96	172,89				
19	2	» »	K	29	101	68,11	101	75,91	76,81	27,00
	3	» »	I_1	27	100	86,19				
20	6	» »	K	28	103	48,67	100	58,39	46,84	636,00
	7	» »	I_1	24	96	44,70				
21	8	» »	K	30	105	49,83	102	67,49	59,34	540,00
	9	» »	I_1	30	99	68,86				
22	13	» »	K	30	100	23,97	97	45,76	37,28	504,00
	14	» »	I_1	26	94	52,72				
23	17	» »	K	28	106	27,93	105	31,82	31,61	40,00
	18	» »	I_1	12	104	40,64				
24	84	Svalöf's early strain	K	14	96	41,31	95	56,82	58,12	14,00
	85	» » »	I_1	21	95	69,05				

Group No.	Field No.	Basic population	Inbreeding generation	Number of plants	Mean height cm.	Variance	Group Mean	Var_t	Var_{ab}	Var_p
25	88	Svalöf's early strain	K	29	92	36,61	90	52,06	33,50	683,00
	89	» » »	I_1	7	81	19,00				
26	93	» » »	K	30	95	46,24	94	39,36	36,44	165,00
	94	» » »	I_1	15	91	16,14				
27	95	» » »	K	28	96	42,52	96	35,03	35,00	36,00
	96	» » »	I_1	9	94	9,63				
28	97	» » »	K	29	88	43,07	84	59,66	40,18	1014,00
	98	» » »	I_1	22	79	36,33				
29	4100	» » »	K	28	95	31,59	92	58,28	36,97	889,00
	1	» » »	I_1	13	85	49,08				
30	5	» » »	K	28	102	64,22	101	53,86	53,68	60,00
	6	» » »	I_1	8	99	13,00				
31	9	» » »	K	27	94	45,19	89	112,16	50,24	2403,00
	10	» » »	I_1	12	77	58,09				
32	11	» » »	K	28	94	50,19	92	56,46	49,95	304,00
	12	» » »	I_1	12	88	49,36				
33	13	» » »	K	29	101	21,11	97	59,17	22,73	1517,00
	14	» » »	I_1	13	88	26,50				
34	42	Svalöf's late strain	K	25	112	67,46	113	62,25	59,32	153,00
	43	» » »	I_1	8	117	31,43				

progenies after self-fertilization than in those after free flowering, then the progenies of two mother plants after isolation have shown a greater average height than corresponding *K*-families. This increase is certainly not so great, in the first case so slight that the intraclass variance is greater than the interclass variance, and the increase has therefore no statistical significance. In the other case, in *Svalöf's late strain*, the increase is greater, resulting in the interclass variance being greater than the intraclass variance in this group. Owing to the small number of D. F. no great statistical significance can however be assigned to this difference, as it might have arisen from purely incidental variation. The decrease in height which appears to have occurred in the other groups, as shown by the average heights in Table 5, does not always stand the statistical test either. In two cases, groups 19 and 24, the interclass variance is lower than the intraclass variance and the decrease here has no significance whatever, and the *I*- and *K*-families in these groups may be considered to belong to the same height population. In 9 other groups (1, 3, 6, 10, 13, 14, 23, 27 and 30) the interclass variance is greater, but the difference is not so great that it could not have arisen incidentally. The remaining 21 groups, however, show such a great decrease in height that it can be proved with statistical

accuracy that a depression has occurred, that is, the differences are so great that they cannot be considered to lie within the limits of chance variation. The first group may be cited as an example, where half the difference between the natural logarithm for var_p and var_{ab} $(= z)$ amounts to 0,7880. In chance variation alone z amounts in 5 % of the cases only to a value of 0,7246 with the number of degrees of freedom in question, showing that considerable statistical significance may be assigned to this difference. In other cases z amounts to a value considerably in excess of that which occurs by chance in 1 per cent of all cases. Thus, it can be proved with the aid of the analysis of variance that in 21 groups out of 34 a depression in height has occurred in families after self-fertilization, whereas in the remaining 13 groups no significant difference is found between families after self-fertilization and after cross-fertilization.

TABLE 6. *Analysis of Variance of Inbreeding Effect in Height within Different Strains of Meadow Fescue in 1929.*

	Intraclass			Interclass		
	Σd^2	D. F.	Variance	Σd^2	D. F.	Variance
Weibull's selected.....	7697,00	154	49,98	661,53	3	220,51
Daehnfeldt's strain	23309,00	430	54,21	1880,56	9	208,95
Weibull's Mimer	23409,00	415	56,41	1600,58	8	200,07
Svalöf's early strain.....	15751,00	382	41,23	1995,92	9	221,77

A close examination of the variability of the inbreeding effect between the different groups of the strains examined will show (Table 6) that in all the strains (in this case it has not been possible to include *Svalöf's late strain*) the interclass variance of the inbreeding effect is greater than the intraclass variance. These differences are, besides, statistically significant in all cases, showing that different mother plants give different inbreeding effect, not only due to incidental variation but also on account of their genotypical constitution. Another striking thing is the close similarity in the size of both intraclass and interclass variance in the different strains (Table 6), and thereby the total variance of the inbreeding effect in the strains tested, which appears further from Table 7. Thus, when the different strains exhibit the same variance in inbreeding effect they may be assumed to have a similar degree of genetic homogeneity with regard to height. Although the absolute inbreeding effect found varies on the average between the

different strains these differences have no significance, as the interclass variance is in this case lower than the intraclass variance (Table 7).

In Table 8, which contains summarizing analysis of variance of each strain separately, we find within each strain a statistically significant depression in the *I*-families as compared with the *K*-families. The variance between families within groups is very significantly greater than the variance within families and it is thus proven that the *I*- and *K*-materials belong to different height populations.

On comparing the variability within *I*-families with that within *K*-families in the same group it will have been seen already in Table 5 that the variance is sometimes greater in the *I*-family and sometimes in the *K*-family. If the total (intra- and inter-family) variance of the whole *I*-material in a strain is compared with the total variance of the

TABLE 7. *Analysis of Variance of Inbreeding Effect in Height between Different Strains of Meadow Fescue in 1929.*

	Number of groups	$\Sigma\left(\frac{n_1 \cdot n_2}{n_1 + n_2}\right)$	Inbreeding effect. Mean, cm.	Σd^2	D. F.	Variance
Weibull's selected	4	37,0	6,7	8358,53	157	53,24
Daehnfeldt's strain	10	98,6	6,2	25189,56	439	57,38
Weibull's Mimer ...	9	102,1	7,2	25009,58	423	59,12
Svalöf's early strain	10	84,1	7,8	17746,92	391	45,39
Total within strains	33	321,8	7,0	76304,59	1410	54,12
Between strains ...	—	—	—	124,34	3	41,45

whole *K*-material in the same strain it will be found that the relation is different in different strains. In *Weibull's selected* the total variance is about equal in both cases, but within the other strains the *I*-material shows a greater variance than the *K*-material. The differences are statistically established, hence it can be shown that the variability within these strains is greater in the *I*-material than in the *K*-material. In all strains the total variance for the *I*-material is 118,75, and for the *K*-material 87,17. The z of the difference amounts to 0,1546, while its 1 % limit in chance variation alone in 544 and 934 D. F. does not go further than 0,0879. A significant difference can therefore be shown between the *I*- and *K*-material.

The combining of the *I*-families within each strain furnishes a material, the total variation of which consists of a very high interfamily variance and an intrafamily variance certainly inferior in comparison. The differentiation between these families is therefore very well-defined.

TABLE 8. *Summarizing Analysis of Variance of the Height of Meadow Fescue Material in 1929.*

	Number			Average height cm.	Σd^2	D. F.	Variance
	Plants	Families	Groups				
Weibull's selected							
After free flowering. *K*	97	4	—	112			
Within families	—	—	—	—	5012	93	53,89
Between »	—	—	—	—	1196	3	398,67
Total.....	—	—	—	—	6208	96	64,67
After isolation. I_1	65	4	—	105	—	—	—
Within families	—	—	—	—	2685	61	44,02
Between »	—	—	—	—	1293	3	431,00
Total	—	—	—	—	3978	64	62,16
Daehnfeldt's strain							
After free flowering. *K*	288	10	—	105	—	—	—
Within families	—	—	—	—	11776	278	42,36
Between »	—	—	—	—	6127	9	680,78
Total	—	—	—	—	17903	287	62,38
After isolation. I_1	162	10	—	99	—	—	—
Within families	—	—	—	—	11533	152	75,88
Between »	—	—	—	—	4346	9	482,89
Total	—	—	—	—	15879	161	93,63
Weibull's Mimer							
After free flowering. *K*	255	9	—	104	—	—	—
Within families	—	—	—	—	12676	246	51,53
Between »	—	—	—	—	1189	8	148,63
Total	—	—	—	—	13865	254	54,59
After isolation. I_1	178	9	—	96	—	—	—
Within families	—	—	—	—	10733	169	63,51
Between »	—	—	—	—	2440	8	305,00
Total	—	—	—	—	13173	177	74,42
Svalöf's early strain							
After free flowering. *K*	270	10	—	95	—	—	—
Within families	—	—	—	—	11010	260	42,35
Between »	—	—	—	—	4195	9	466,11
Total	—	—	—	—	15205	269	56,52
After isolation. I_1	132	10	—	87	—	—	—
Within families	—	—	—	—	4741	122	38,86
Between »	—	—	—	—	6114	9	679,33
Total	—	—	—	—	10855	131	82,86

Such a differentiation is, however, prevalent also between the families after free flowering.

On analyzing the variance within the *I*- and *K*-material the inter-

family variance in *Weibull's selected*, *Weibull's Mimer* and *Svalöf's early* is found to be greater in the *I*-material than in the *K*-material, but the relation is the reverse in *Daehnfeldt's strain*. In none of these cases is the difference so great that there is any statistical significance for

TABLE 9. *Summarizing Analysis of Variance of the Whole Meadow Fescue Material with the Exception of Svalöf's late strain.*

	Number			Mean height cm.	Σd^2	D. F.	Variance
	Plants	Families	Groups				
Families after free flowering. K.	901	33	—	102	—	—	—
Within fam. within strains	—	—	—	—	40474	877	46,15
Between fam. within st.	—	—	—	—	12707	29	438,17
Total within strains	—	—	—	—	53181	906	58,70
Between strains	—	—	—	—	26542	3	8847,33
Total	—	—	—	—	79723	909	87,70
Families after isolation. I_1	537	33	—	96	—	—	—
Within fam. within strains	—	—	—	—	29692	504	58,91
Between fam. within st.	—	—	—	—	14193	29	489,41
Total within strains	—	—	—	—	43885	533	82,34
Between strains	—	—	—	—	18549	3	6183,00
Total	—	—	—	—	62434	536	116,48
K-and I_1-families in groups	1447	68	34	100	—	—	—
Within fam. within gr. within st.	—	—	—	—	70174	1381	50,81
Between fam. within gr. within st.	—	—	—	—	21173	33	641,61
Total within groups within st.	—	—	—	—	91347	1414	64,60
Between gr. within st.	—	—	—	—	21525	29	742,24
Total within strains	—	—	—	—	112872	1443	78,22
Between strains	—	—	—	—	37303	3	12434,33
Total	—	—	—	—	150175	1446	103,86

its existence. Neither can any positive difference be shown by combining the strains. This is therefore a further proof that in this material the differentiation is not greater between *I*-families than between *K*-families. The intrafamily variance in *Weibull's selected* and *Svalöf's early* is greater in the *K*-material, but in the other strains it is greater in the *I*-material, although it is only possible to demonstrate a

significant difference in *Daehnfeldt's strain*. In combining the material the intrafamily variance of the *I*-material is 58,54, and of the *K*-material 46,72. z is equal to 0,1128, while its 1 % limit in chance variation remains at 0,0901.

Finally, in Table 9 it will be seen that the variation between the strains is not greater in the *I*-material than in the *K*-material. On the contrary, it is greater in the *K*-material, although this cannot be proved with statistical significance. At the end of Table 9 the entire material has been combined into groups, from which it will be seen that the differentiation between the groups within all the strains is very great and of the same size order as between the families within the groups. This differentiation between the groups is found in each strain separately, although the values of variance are published only for the entire material combined. That the differentiation between the groups is due to the influence of the mother plants is proved by the correlation between mean heights of *I*- and *K*-families in the same group. The strength of this correlation has not been numerically determined but that it is considerable may be inferred from the variance values of Tables 6 and 8. If there were no correlation between mean heights of *I* and *K* in the same group the interclass variance of inbreeding effect (*K*-height—*I*-height) would be approximately equal to the sum of interfamily variances in *I* and *K*. Now the interclass variance of inbreeding effect is considerably lower than this sum, which proves the existence of a correlation between *I*- and *K*-families from the same mother plant. Further, it will be found that there is a very great variation between the strains, as compared with the variation found within the strains. This has already appeared from the means of the individual strains given in Table 8, but full assurance is acquired here that the strains as represented in this material are quite different as regards height.

If we then proceed to investigate whether there is any correlation between the absolute inbreeding effect observed and the variation within the *I*-families, it should perhaps first be called to mind that between the different strains there are no sure differences in the determined inbreeding effect (cp. page 21), and therefore it may be permissible to calculate a correlation for the entire material at once. Between the inbreeding effect and the variance within the *I*-family is found a slight positive correlation, $r = + 0{,}2450$, which has no great statistical significance, but can be attained in about 15 cases out of 100 by chance.

After computing the regression we now find that the variation in inbreeding effect between different groups in the entire meadow fescue material can be analyzed in the following manner:

	Σd^2	D. F.	Variance
Total interclass	7117,35	33	215,68
Regression upon variance in I_1..	441,36	1	441,36
Remaining interclass	6675,99	32	208,62
Intraclass	72005,05	1412	51,00

That part of the total variance in inbreeding effect which is correlated with the variance in the I_1-families is therefore considerably greater than the remaining interclass variance, but the difference is not statistically significant, since z is only 0,3747, whereas by chance it reaches a value of about 0,71 once in 20 cases. Between the remaining interclass and the intraclass variance there is a significant difference.

c) REVIEW OF THE RESULTS.

Fertility.

The seed setting on isolation is generally low, varying between 0 and 11,3 % in the plants, where exact counts were made. The differences between the plants are significant and cannot be due only to chance variation.

There is also a great variation in seed setting on open flowering, values between 18,7 and 84,4 % being obtained in the above mentioned plants.

There is a positive correlation between the percentage seed setting on isolation and on free flowering, although because of the small number of plants the coefficient is not very significant.

The mathematical analysis has shown, however, that there is a considerable variation in isolation-fertility independent of the variation in general fertility, as measured by the percentage of seed setting on open flowering.

Inbreeding effects.

Chlorophyll-deficient seedlings are rather common. They are of different types such as white, yellow, yellowish green and striated, indicating several different genetical factors. The numbers have been too small, however, to permit any factorial analysis.

Concerning several characters which were not made subjects of

definite measurements a great variation was noted in the inbred material, greater than in the progenies after free flowering.

In 21 out of 34 investigated cases a significant decrease in height was observed as a result of inbreeding. In 11 other cases the decrease was not statistically significant. In two cases an insignificant increase in height was observed.

The inbreeding effect in height was different after different mother plants, these differences being statistically significant.

There were no significant differences between the average inbreeding effects in height of the four commercial strains investigated. Nor were there any differences between these strains as regards the variability in inbreeding effect after different mother plants.

In three of the strains the variability in height in the inbred families was significantly greater than in the corresponding *K*-families. In the fourth strain no significant difference was observed in this respect.

The mean heights of the progenies of different mother plants were widely and significantly different. This holds true for the *K*-material as well as for the *I*-material and no difference could be demonstrated between the two groups of material as regards the degree of differentiation between different progenies.

If the *K*- and *I*-progenies from the same mother plant are combined into groups these groups form well defined and different height populations. This indicates that the genetical constitution of the mother plant greatly influences the *K*- as well as the *I*-progeny. This influence is further proved by the existence of a marked correlation between the mean heights of *I*- and *K*-families in the same group.

There is a rather uncertain positive correlation between the degree of inbreeding effect and the degree of variability in the *I*-families.

2. DACTYLIS GLOMERATA L., COCKSFOOT.

a) FERTILITY.

Isolations of cocksfoot were made at the same time and by the same method as in meadow fescue. No exact counts were made of the degree of fertility. The seed setting could, however, be estimated to some degree, partly in threshing the isolations and partly by the number of seedlings appearing after sowing in 1927. From these observations the variation in »self-fertility» appeared to be still greater in cocksfoot than in meadow fescue. No progenies were obtained from

a great number of isolations, while in others more than 500 seeds could be harvested. The variability seems to embrace complete sterility with every type of transition to almost complete self-fertility, which accords well with the results SYLVÉN (1929) and STAPLEDON (1931) obtained on a very large material.

b) THE EFFECT OF SELF-FERTILIZATION ON THE PROGENY.

As a typical effect of inbreeding a large number of chlorophyll variants appeared already in the seedling stage. These recessive segregating products occurred most commonly in the strains *Tardus* and *Minerva II*. Thus, there appeared pure albino, yellow, yellowish green and striated types, the first two types of course being unable to survive the seedling stage while the others showed rather good vigour and in the course of the summer assumed an almost entirely green colour, making them hardly distinguishable from normally green individuals. Besides single specimens of such chlorophyll-deficient variants in most families large numbers were also observed in some families. The figures obtained in three *Tardus* families and two *Minerva II* were as follows:

	Albino	Yellow	Green	Total
Tardus	12	21	185	218
»	3	—	40	43
»	—	10	82	92
Minerva II	16	5	922	943
»	4	—	95	99

These figures show that several factors, multiple and possibly even homomeric, are evidently active in the normal development of chlorophyll. Even in this case the observations made are fully in agreement with the results obtained by STAPLEDON (1931).

As for other characters a greater variation has been noted in *I*-material than in *K*-material concerning tillering, length and breadth of leaves, length and form of panicle and height of plant, which latter character was closely analysed. With regard to tillering, extreme types have been met with, which only shoot one or two fertile straws in otherwise vigorous tussocks. These plants prove themselves, besides, to be low and most frequently consist of most extreme minus variants in height. Such types were observed in every strain, sometimes in *I*-families, sometimes in *K*-families, which shows that even after free flowering a segregation of extremes takes place, either due to a certain

self-fertilization or as a result of a cross between plants that are heterozygous in the same factor or factors.

Panicle.

The form and size of the panicle is of great importance in the practical seed-growing of cocksfoot grass, and therefore great attention has been devoted to this item in these investigations. The strains *Tardus* and *413*, the latter raised from *Tardus*, differ quite considerably from the other strains in their special type of panicle. It is somewhat compressed, short and plumpy with short panicle branches, which forms the panicle into a clumpy agglomerate. In such an agglomerate fertilization is probably hampered and it may also hinder the development of the seeds. Experience of experiments as well as seed growing on a large scale with *Tardus* shows that this strain always produces a low yield of seeds and the seeds are also poorly developed. Strain *413* is more extreme in this respect and is therefore a dead loss in seed growing. The seeds never acquire the characteristic tint of cocksfoot when ripe, but remain green and their power of germination does not reach higher than 50 %. In the progenies of both *Tardus* and *413* after isolation there occur quite commonly still more extreme, knotted types, which in a great number of cases show themselves to be quite sterile. This phenomenon of inbreeding must be regarded as a segregation of recessive forms which are eliminated in the next generation, as they are not capable of producing progeny, or at least only a very few. The abnormal development of the floral parts, at least externally rather similar to true vivipary, which in rainy summers is not uncommon in cocksfoot grass, very frequently occurred in this type, probably on account of their capacity in rainy weather to retain the moisture within the panicles to a greater extent than sparsely panicled forms.

Height.

The character that has been most extensively analysed in the cocksfoot material is, however, the height. Measurements were made during the flowering period in 1929, when the plants were two years old and might be considered to have reached full development. As in meadow fescue measurements were made parallelly on families after isolation and after free flowering. In Table 10 will be found the mean heights of each family, along with the number of plants and the variances in the different families. Examining the material in its entirety it will be

TABLE 10. *Analysis of Variance of the Height of Inbreeding Material in Cocksfoot in 1929.*

Group No.	Field No.	Basic population	Inbreeding generation	Number of plants	Mean height cm.	Variance	Group average	$Var._t$	$Var._{ab}$	$Var._p$
1	2819	Skandia cocksfoot	K	29	123	58,29	118	129,95	60,89	2685,00
	20	» »	I_1	10	104	69,00				
2	21	» »	K	25	121	130,75	117	176,48	116,89	1845,00
	22	» »	I_1	5	100	33,75				
3	25	» »	K	30	108	55,76	100	237,76	69,90	7120,00
	26	» »	I_1	13	80	104,08				
4	29	» »	K	27	114	105,69	111	219,19	164,40	1863,00
	30	» »	I_1	5	93	546,00				
5	31	» »	K	29	114	150,54	113	127,34	128,62	57,00
	32	» »	I_1	28	112	105,89				
6	39	» »	K	29	122	108,96	111	369,41	216,46	8017,00
	40	» »	I_1	23	97	353,27				
7	41	» »	K	30	109	91,86	104	141,71	91,52	2350,00
	42	» »	I_1	16	94	90,87				
8	43	» »	K	29	117	104,04	115	125,06	94,72	1096,00
	44	» »	I_1	5	101	29,50				
9	45	» »	K	29	117	103,46	114	116,41	90,03	987,00
	46	» »	I_1	6	103	14,80				
10	65	Minerva II cocksfoot, I_1	K	29	114	54,29	107	162,54	67,38	3969,00
	66	» » »	I_2	13	93	97,92				
11	74	» » »	K	28	105	37,19	100	146,84	77,03	2660,00
	75	» » »	I_2	10	86	196,44				
12	77	» » »	K	30	110	79,21	105	100,43	70,72	1794,00
	78	» » »	I_2	29	99	61,93				
13	84	» » »	K	29	122	53,96	122	72,44	74,29	8,00
	85	» » »	I_2	8	121	155,57				
14	86	» » »	K	29	120	63,64	113	144,30	96,15	2793,00
	87	» » »	I_2	28	106	129,85				
15	3023	Tardus cocksfoot	K	25	118	146,17	119	126,73	126,93	121,00
	24	» »	I_1	6	123	34,75				
16	25	» »	K	27	127	164,00	128	132,29	133,70	56,00
	26	» »	I_1	29	129	105,57				
17	27	» »	K	27	128	109,23	128	105,81	107,60	22,00
	28	» »	I_1	22	127	105,57				
18	29	» »	K	26	121	71,24	117	100,92	86,25	864,00
	30	» »	I_1	28	113	100,15				
19	31	» »	K	29	123	115,14	122	188,75	184,87	110,00
	32	» »	I_1	27	120	259,96				
20	34	» »	K	28	116	81,67	112	219,88	122,00	3352,00
	35	» »	I_1	6	90	339,80				
21	37	» »	K	29	102	128,54	100	136,33	135,46	172,00
	38	» »	I_1	14	98	150,38				
22	39	» »	K	29	131	59,61	129	101,23	98,89	232,00
	40	» »	I_1	29	127	138,18				
23	41	» »	K	29	119	143,82	116	246,58	233,81	936,00
	42	» »	I_1	27	111	330,73				
24	44	» »	K	26	120	82,84	118	122,43	109,10	509,00
	45	» »	I_1	5	109	273,25				

Group No.	Field No.	Basic population	Inbreeding generation	Number of plants	Mean height cm.	Variance	Group average	Var_t	Var_{ab}	Var_p
25	3223	Strain 413, I_1	K	28	119	99,78	109	193,53	102,90	4906,00
	24	» » »	I_2	26	100	106,28				
26	28	» » »	K	28	120	173,37	115	292,05	227,95	2728,00
	29	» » »	I_2	12	102	361,82				
27	30	» » »	K	26	112	157,96	110	136,24	135,45	168,00
	31	» » »	I_2	16	108	97,93				
28	32	» » »	K	13	114	68,16	103	282,45	78,11	4165,00
	33	» » »	I_2	8	85	95,14				
29	35	» » »	K	28	120	39,04	113	225,70	165,57	2992,00
	36	» » »	I_2	20	104	345,37				
30	39	» » »	K	27	120	45,00	115	201,03	52,14	4519,00
	40	» » »	I_2	4	84	114,00				
31	41	» » »	K	25	107	115,87	95	437,69	115,57	11712,00
	42	» » »	I_2	12	69	114,91				
32	43	» » »	K	29	117	132,57	115	138,63	136,28	233,00
	44	» » »	I_2	13	112	144,92				
33	45	» » »	K	24	116	102,61	108	239,91	81,97	5136,00
	46	» » »	I_2	9	88	22,63				
34	47	» » »	K	23	114	137,77	109	287,85	166,04	3455,00
	48	» » »	I_2	5	85	321,50				
35	51	» » »	K	29	102	114,43	99	168,71	119,68	1836,00
	52	» » »	I_2	7	84	144,17				
36	3339	Strain 453, I_1	K	29	131	84,36	128	119,43	103,25	702,00
	40	» » »	I_2	9	121	169,38				
37	43	» » »	K	29	125	119,82	126	143,82	143,94	137,00
	44	» » »	I_2	27	128	169,92				
38	45	» » »	K	28	124	99,56	123	87,98	88,89	47,00
	46	» » »	I_2	19	122	72,89				
39	47	» » »	K	28	134	100,89	136	112,73	108,00	373,00
	48	» » »	I_2	29	139	114,86				
40	49	» » »	K	24	141	192,04	142	122,65	124,59	24,00
	50	» » »	I_2	29	142	69,18				
41	51	» » »	K	28	144	51,41	141	70,67	57,10	627,00
	52	» » »	I_2	15	136	68,07				
42	55	» » »	K	25	123	192,88	124	262,45	256,46	430,00
	56	» » »	I_2	5	130	633,00				
43	59	» » »	K	27	131	100,58	131	121,24	122,94	29,00
	60	» » »	I_2	29	132	143,71				

seen that so-called inbreeding effect has occurred in most of the groups, *i. e.* the *I*-families differ from the *K*-families in height. This effect, however, varies very much in the different groups and in the different strains. Glancing at the last two columns in Table 10, showing the intrafamily and interfamily variances of the separate groups, it will be seen that the interfamily variance is in general greater than the corresponding intrafamily variance, even if the differences are not always so great that they can be shown to be significant.

On examining the individual strains it will appear that in *Skandia* there are 8 groups in which the interfamily variance is statistically greater than the intrafamily variance. The probability in each separate instance that a real difference is present is more than 99 : 1. Hence, it can be considered established that inbreeding in these groups has brought about a depression in height, as compared with the progeny after free flowering. In Group number 5 the means also show a reduction in height in the inbred family, but here the difference in height has no statistical significance.

All the five groups in *Minerva II* also exhibit an inbreeding effect, which in four of them can be shown not to have arisen from chance variation alone. In the fifth group (No. 13) the difference in height has no significance.

Tardus differs from *Skandia* and *Minerva II* in that the different groups exhibit a very varying inbreeding effect. Only in 4 of the 10 groups, namely 18, 20, 23 and 24, is it possible to ascertain a depression with any degree of certainty. The others exhibit no significant differences in height; in fact the greatest height is present in the inbred families of two of the groups. Strain *413* shows a depression in all the 11 groups, statistically significant in nine of them, while Strain *453* gives a depression in 3 groups and a luxuriation in 5. The luxuriation cannot, however, in any of the cases be shown not to have arisen from chance variation, although the differences in both groups are rather great. The depression on the other hand is significant in two cases (Nos. 36 and 41).

The result of this analysis thus shows that the inbreeding effect is not so universal as might be assumed and as the combined material would indicate. A significant inbreeding effect can be shown in only 27 of the 43 groups examined.

Thus, the inbreeding effect varies in the progenies of different mother plants, which is further borne out by Table 11, in which is given a summary of the intraclass and interclass variances of the inbreeding effect in each strain separately. The interclass variance is generally greater and the differences are so great that they cannot be assumed to have been brought about by chance variation alone. It is also clear from Table 11 that the individual strains do not exhibit the same variance of inbreeding effect as was the case in meadow fescue, but they show instead great diversity in the variances. This indicates therefore that the various strains, as here represented, really have different degrees of genetic homogeneity. That they also differ in

average inbreeding effect is shown by Table 12. The mean inbreeding effects of the individual strains are widely different and the inter-strain variance is significantly larger than the variance within the strains. It can therefore be considered very probable that the strains examined here differ with respect to inbreeding effect. *Minerva II* differs from

TABLE 11. *Analysis of Variance of Inbreeding Effect in Height within the Various Strains of Cocksfoot.*

	Intraclass			Interclass		
	Σd^2	D. F.	Variance	Σd^2	D. F.	Variance
Skandia	41250,00	350	117,86	5371,40	8	671,43
Minerva II	17387,00	223	77,97	1809,90	4	452,50
Tardus	61212,00	448	136,63	4005,84	9	445,09
Strain 413	50466,00	390	129,40	9464,93	10	946,59
Strain 453	43945,00	364	120,73	2119,88	7	302,84

the other strains in having a lower variation, which does not seem possible either to be due to any incidental circumstance.

In Table 13 the *I*- and the *K*-families have again been combined separately within each strain, whereby it is ascertained that the families

TABLE 12. *Analysis of Variance of Inbreeding Effect in Height between Different Strains of Cocksfoot.*

	Number of groups	$\Sigma\left(\frac{n_1 n_2}{n_1 + n_2}\right)$	Inbreeding effect Average cm.	Σd^2	D. F.	Variance
Skandia	9	71,9	17,0	46621,40	358	130,23
Minerva II	9	51,6	13,5	19196,90	227	84,57
Tardus	10	105,6	4,6	65217,84	457	142,71
Strain 413	11	83,3	19,5	59930,93	400	149,83
Strain 453	8	87,5	−0,7	46064,88	371	124,16
Total within strains	43	401,9	10,0	237031,95	1813	130,74
Between strains	—	—	—	24950,70	4	6237,68

are differentiated in both the *I*-material and the *K*-material, since in both cases the variation between the families is considerably greater than within them, and the differences exceed the limits of chance variation.

Then, comparing the variability in the *I*-material, on the one hand, and in the *K*-material, on the other, it will be seen from Table 14 that

TABLE 13. *Summarizing Analysis of Variance of the Height in Cocksfoot Material.*

	Number			Mean height cm.	Σd^2	D. F.	Variance
	Plants	Families	Groups				
Skandia							
After free flowering. *K*	257	9	—	116	—	—	—
Within families	—	—	—	—	24875	248	100,30
Between »	—	—	—	—	6762	8	845,25
Total	—	—	—	—	31637	256	123,58
After isolation. I_1	111	9	—	99	—	—	—
Within families	—	—	—	—	16375	102	160,54
Between »	—	—	—	—	10468	8	1308,50
Total	—	—	—	—	26843	110	244,03
Minerva II							
After free flowering. *K*	145	5	—	114	—	—	—
Within families	—	—	—	—	8114	140	57,96
Between »	—	—	—	—	5648	4	1412,00
Total	—	—	—	—	13762	144	95,57
After isolation. I_2	88	5	—	102	—	—	—
Within families	—	—	—	—	9273	83	111,72
Between »	—	—	—	—	7210	4	1802,50
Total	—	—	—	—	16483	87	189,46
Tardus							
After free flowering. *K*	275	10	—	120	—	—	—
Within families	—	—	—	—	29188	265	110,14
Between »	—	—	—	—	14848	9	1649,78
Total	—	—	—	—	44036	274	160,72
After isolation. I_1	193	10	—	118	—	—	—
Within families	—	—	—	—	32024	183	174,99
Between »	—	—	—	—	20630	9	2292,22
Total	—	—	—	—	52654	192	274,24
Strain 413.							
After free flowering. *K*	280	11	—	115	—	—	—
Within families	—	—	—	—	29454	269	109,49
Between »	—	—	—	—	9434	10	943,40
Total	—	—	—	—	38888	279	139,38
After isolation. I_2	132	11	—	96	—	—	—
Within families	—		—	—	21012	121	173,65
Between »	—	—	—	—	20241	10	2024,10
Total	—	—	—	—	41253	131	314,91
Strain 453.							
After free flowering. *K*	218	8	—	132	—	—	—
Within families	—	—	—	—	24178	210	115,13
Between »	—	—	—	—	11382	7	1626,00
Total	—	—	—	—	35560	217	163,87

	Number			Mean height cm.	Σd^2	D. F.	Variance
	Plants	Families	Groups				
After isolation. I_2	162	8	—	133	—	—	—
Within families	—	—	—	—	19767	154	128,34
Between »	—	—	—	—	7872	7	1124,57
Total	—	—	—	—	27639	161	171,67

the total variance of the *I*-material is considerably greater than that of the *K*-material, there being statistical certainty for the existence of this difference. On analysing the variation within the *I*- and *K*-material it will be found that both intra-family and inter-family variance is greater in the inbred material. The intrafamily variances are 153,11 and 102,30 respectively. z is 0,2016 and its 1 % limit in chance variation alone is not more than 0,0805. The inter-family variances are 1747,92 and 1265,11 respectively. The difference between them, however, is not great enough for any significance to be assigned to it. Thus, it is only the intra-family variance that is significantly greater in the *I*-material than in the *K*-material, which implies that the differentiation between the plants is greater in the *I*-families. With the exception of strain *453*, all strains are alike and show individually the same difference in the intrafamily variance of the *I*- and *K*-families as that shown by the material in its entirety, but no significant difference can be shown between the interfamily variances. Strain *453* differs from the other strains in that no differences can be ascertained in either the intra-family or interfamily variances, the differences in this case being within the limits of chance variation (Table 13).

As in meadow fescue, a wide differentiation can thus be shown in cocksfoot between the families even after free flowering. In the material examined it cannot be proved that the differentiation in height should be greater between *I*-families than between corresponding *K*-families, even if the difference found in degree of differentiation is suggestive (Table 14).

As is shown in Table 14 the groups are well defined, the intergroup variance being here as in meadow fescue of about the same size as the interfamily variance within the groups. The existence of a rather marked correlation between mean height of *I*- and *K*-families of the same group is proved in the same manner as in meadow fescue, viz. by a comparison of the interclass variance of the inbreeding effect and the

sum of interfamily variances in *I*- and *K*-material. Thus, even in cocksfoot it is proved that *I*- and *K*-family pairs from the same mother plant form well defined height populations.

TABLE 14. *Summarizing Analysis of Variance of the Height in the whole Cocksfoot Material.*

	Number			Mean height cm.	Σd^2	D. F.	Variance
	Plants	Families	Groups				
All strains							
Families after free flowering. K	1175	43	—	119	—	—	—
Within fam. within strains	—	—	—	—	115809	1132	102,30
Between fam. within strains	—	—	—	—	48074	38	1265,11
Total within strains	—	—	—	—	163883	1170	140,07
Between strains	—	—	—	—	47535	4	11883,75
Total	—	—	—	—	211418	1174	180,08
Families after isolation. I_1 and I_2	686	43	—	112	—	—	—
Within fam. within strains	—	—	—	—	98451	643	153,11
Between fam. within strains	—	—	—	—	66421	38	1747,92
Total within strains	—	—	—	—	164872	681	242,10
Between strains	—	—	—	—	139741	4	34935,25
Total	—	—	—	—	304613	685	444,69
K- and I-families in groups	1861	86	43	117	—	—	—
Within fam. within gr. within st.	—	—	—	—	214260	1775	120,71
Between fam. within gr. within st.	—	—	—	—	87837	43	2042,72
Total within gr. within st.	—	—	—	—	302097	1818	166,17
Between groups within strains	—	—	—	—	91314	38	2403,00
Total within strains	—	—	—	—	393411	1856	211,97
Between strains	—	—	—	—	144240	4	36060,00
Total	—	—	—	—	537651	1860	289,05

A very great variation in mean height occurs between the strains, which, as shown by Table 14, seems to be considerably greater than the variation within the strains. It can also be shown with statistical significance that this is the case, hence each strain may be considered

to form a separate height population. The same thing can be shown within both the *I*- and the *K*-material. Comparing the variances between the strains in the entire *I*-material, on the one hand, and in the entire *K*-material, on the other hand, it would appear as if the differentiation after isolation was greater than that after free flowering, but no positive proof of this can be obtained with this number of D. F. There is an indication, however, that this is the case (Table 14).

If we now examine whether there is any correlation between the inbreeding effect and the variance in the *I*-families we obtain the following correlations:

Strain	Number of Pairs	r
Skandia	9	$+ 0{,}2782$
Minerva II	5	$- 0{,}0133$
Tardus	10	$+ 0{,}6820$
413	11	$- 0{,}1385$
453	8	$- 0{,}5086$

Although none of these coefficients of correlation, except that for *Tardus*, with a probability of 90 : 10, are of any statistical significance individually and thus no correlation can be proved to exist between the inbreeding effect and the variance in the *I*-families within the different strains, it is nevertheless interesting to observe that *Skandia* and *Tardus* give positive correlations while the others give negative. As already mentioned, *Skandia* and *Tardus* have been least subjected to previous inbreeding and form a group by themselves, as compared with the other strains, which must be considered to belong to a later inbreeding generation. It now appears as if this should have an influence on the correlation between the inbreeding effect and the variance in the *I*-families. As these two groups may be separated biologically from one another it may be proper to investigate the correlation within each group separately. The first point to be discerned is that there is no significant difference between the correlations in *Skandia* and *Tardus* and it will therefore be deemed permissable to compute an average correlation for these strains. The coefficient of correlation then obtained for this group is $r = + 0{,}5229$, which is fairly significant, and so it might be maintained that a positive correlation really exists. The probability at any rate that this is the case is 95 to 5. Even within the other group no significant difference is found between the correlations of the various strains, hence an average correlation has also been computed for this group. This

TABLE 15. *Height Distribution in Various Families of Strain 453.*

Group No.	Family No.	Inbreeding generation	Number of Individuals in Different Height Classes																			Total	Mean height
			70—75	75—80	80—85	85—90	90—95	95—100	100—105	105—110	110—115	115—120	120—125	125—130	130—135	135—140	140—145	145—150	150—155	155—160	160—165		
1	3339	K	—	—	—	—	—	—	1	—	1	2	4	3	8	8	1	—	1	—	—	29	131
	40	I_2	—	—	—	—	—	—	2	—	1	2	—	2	1	1	—	—	—	—	—	9	121
2	43	K	—	—	—	—	1	—	—	2	1	6	3	5	7	3	1	—	—	—	—	29	125
	44	I_2	—	—	—	—	—	—	1	1	2	7	2	3	2	5	1	1	2	—	—	27	128
3	45	K	—	—	—	—	—	1	—	2	2	3	5	8	3	4	—	—	—	—	—	28	124
	46	I_2	—	—	—	—	—	—	1	1	2	4	5	2	3	1	—	—	—	—	—	19	122
4	47	K	—	—	—	—	—	—	—	—	2	2	2	2	6	6	4	4	—	—	—	28	134
	48	I_2	—	—	—	—	—	—	—	1	—	1	1	3	2	9	4	3	5	—	—	29	139
5	49	K	—	—	—	—	1	—	—	—	—	—	1	2	1	2	8	4	3	1	1	24	141
	50	I_2	—	—	—	—	—	—	—	—	—	1	—	3	2	6	5	7	5	—	—	29	142
6	51	K	—	—	—	—	—	—	—	—	—	—	—	1	3	5	4	10	5	—	—	28	144
	52	I_2	—	—	—	—	—	—	—	—	1	—	—	1	6	3	3	1	—	—	—	15	136
7	55	K	1	—	—	—	—	—	1	—	4	2	4	5	4	4	—	—	—	—	—	25	123
	56	I_2	—	—	—	1	—	—	—	—	—	—	—	—	—	2	2	—	—	—	—	5	130
8	59	K	—	—	—	—	—	—	—	—	2	3	4	3	4	5	6	—	—	—	—	27	131
	60	I_2	—	—	—	—	—	—	1	1	1	2	3	2	6	7	3	3	—	—	—	29	132

amounts to $r = -0{,}3832$ with about the same ratio of probability of the existence of a correlation as in the first group. If the correlations within these groups of strains, that is, in I_1-material and I_2-material, are then compared it will be found that the correlations are so divergent that the groups are quite differentiated from one another. The difference of the values of z amounts to $0{,}9841$ with a standard error of $\pm 0{,}3789$, and therefore there is a considerable probability that the inbreeding effect and variance of I are correlated differently in the two groups.

In order to illustrate the variation in the progenies of mother plants with and without any inbreeding effect the number of variants within the different height classes of each individual family of strain *453* has been tabulated in Table 15.

c) REVIEW OF THE RESULTS.

Fertility.

Great variation between different plants was observed in the degree of seed setting on isolation but exact counts were not made.

Inbreeding effects.

Chlorophyll-deficient seedlings of the same types as in meadow fescue were obtained. In some cases the numbers were sufficiently large to warrant the conclusion that the segregation is not a monofactorial one.

A great variation was noted in several characters in *I* as well as in *K* families. Although exact measurements were not made it was stated that in several cases the variation was greater in *I* than in *K* families. Especially concerning tillering, length and breadth of leaves, and length and type of panicle the variation was observed to be very great. An extreme, sterile tussock type, giving no straws with panicles, was observed both in *I* and *K* families.

The strains *Tardus* and *No. 413*, the latter derived from *Tardus*, are characterized by a very short, clumpy panicle, from which quite normal seeds never develop, the seeds obtained being small, green and with low germination capacity. After isolation more extreme, contracted panicle types occur with very low degree of fertility. In the rainy autumn of the year 1927 an observation was made on the abnormal development of the cocksfoot panicles, giving green leaves

in the flowers resembling the bulbils of viviparous forms, and the short, clumpy panicle type seemed to develop this abnormality more frequently.

By comparing mean heights of *I* and *K* families a significant height depression was observed in 27 out of 43 *I* families, in 9 cases an insignificant decrease and in 7 cases a slight height increase but without significance was obtained.

The inbreeding effect in height was found by mathematical analysis to be significantly different after different mother plants. The average inbreeding effect was different in different strains, these differences also being statistically significant. The variation in the degree of inbreeding effect differs in size in different strains, which was not the case in meadow fescue.

The intraclass variance of the height of the *I* families is greater than that of the *K* families in all the strains except in *No. 453*, where the difference is insignificant. This strain shows, on an average, a smaller inbreeding effect in height than the other strains.

The mean heights of the progenies of different mother plants are significantly different in the *I* as well as in the *K* material. The differentiation between the families is in this case suggestively larger in the *I* than in the *K* material.

By grouping the *I* and *K* progenies from the same mother plant we find that these groups form well defined and different height populations. This indicates that the genetical constitution of the mother plant greatly influences the *K* as well as the *I* progeny, which is further proved by the existence of a marked correlation between the mean heights of *I* and *K* families in the same group.

The correlation between the degree of inbreeding effect and variance in the *I* families varies between the strains investigated. In two strains, *Skandia* and *Tardus*, the correlation is positive, in the other three strains it is found to be negative. When the strains are divided into two groups with positive and negative correlations respectively a fairly significant correlation for each group is obtained. The difference in these correlations is significant and therefore the strain groups are deemed differently correlated in respect of inbreeding effect and variability in *I* families. Of the two groups of strains the one with a positive correlation between inbreeding effect and variance in *I* includes strains which belong to the I_0 generations. The strains with a negative correlation, on the other hand, consist of I_1 generations.

3. PHLEUM PRATENSE L., TIMOTHY.

a) FERTILITY.

Experiments in 1925.

»*Self-fertility*». — Already in 1925 some isolations had been performed by Mr. BERG on the material subjected to examination later on. These isolations, which had been harvested but not threshed when Dr. KRISTOFFERSON and the present writer took over the material, consisted of 21 plants of strain *404* and 15 plants of strain *121*, selected as valuable types for practical breeding. Although no careful examination was made of the seed setting in these isolations a great variation was observed when the plants were threshed in the number of seed produced by the different plants and also by the different strains. Thus, it was evident that the isolated plants of strain *121* showed a better seed setting than the plants derived from strain *404*. In the former strain no plant failed entirely to produce seed, although the number set by the different plants varied considerably. Of the plants isolated in strain *404* five yielded no seed at all and five were almost entirely without seed. The other plants produced a more or less abundant progeny, a very good seed setting being recorded for one plant. The observations made therefore indicate varying degrees of »self-fertility» in different individuals and different strains.

Experiments in 1926.

»*Self-fertility*». — In 1926 a large number of isolations were made on material sown in the preceding year by Mr. BERG. All these isolations were performed for practical breeding purposes. Thus, individuals were selected which phenotypically exhibited economically valuable characteristics, such as good height, profuse tillering, leafiness, etc. The number of plants isolated in the various strains was as follows: —

Swedish Common Commercial	16	plants
Kämpe	14	»
Gloria	8	»
Strain 121	21	»
Strain 397	1	plant

As was the case in 1925 no accurate tests were performed either in 1926 on »self-fertility», the seed setting being graded simply by estimation of the number of seed in each isolated plant. The records

show that 4 plants gave no seed at all, 2 gave 1 seed each, in 36 the yield was poor, in 6 fairly good, in 6 good and in 4 very good. Of the last-mentioned 4 plants 3 of them belonged to strain *121* and one to *Common Commercial*. Of the »self-sterile» plants 3 were derived from *Kämpe* and one from *Gloria*. No significant differences could be observed between the strains as each strain contained plants with quite different degrees of seed setting. Assuming that the number of seed recorded is on the whole due to the capacity of self-fertilization of the different individuals and not to casualities and modifications it seems as if *Kämpe* contained more »self-sterile» types and strain *121* more »self-fertile» types than the other strains.

TABLE 16. *Seed Setting in Timothy Isolations in 1927.*

Strain	Number of seeds per panicle, average														Total	Average seed per panicle
	0	0,1—1	—10	—20	—30	—40	—50	—60	—70	—80	—90	—100	—200	>200		
Kämpe.....	15	8	7	2	1	—	—	—	—	—	—	—	—	—	33	2,4
Strain 121.	6	12	13	6	4	2	—	3	—	2	—	—	7	2	57	44,0
Gloria	1	—	4	—	1	—	—	—	1	1	—	—	1	—	9	35,7
Strain 397.	1	1	7	1	1	1	—	—	1	—	—	—	—	—	13	13,4
Finnish ...	—	—	2	—	1	1	—	—	—	—	—	—	1	—	5	36,3
Russian ...	—	3	1	—	—	—	—	—	—	—	—	—	—	—	4	1,3
Total	23	24	34	9	8	4	—	3	2	3	—	—	9	2	121	27,3

Experiments in 1927.

»Self-fertility». — In 1927 a large number of isolations were made on plant material sown in 1926. As formerly the mother plants were selected for their practical breeding qualities. In threshing the number of seed in each panicle was counted and, as a rule, measurements were taken of the length of the panicles so as to be able to estimate seed setting per unit of panicle length.

Altogether 121 plants of various strains were examined, the results are summarized in Table 16. As appears from this table in which the seed setting is given in the number of seed per panicle, as the length of the panicles was not determined on all the plants, the seed set varies very much between the different plants and between the strains. The average seed setting for all plants amounts to 27,3 seeds per panicle, which must be considered a very low degree of »self-fertility». The variation is, however, very great, ranging from 0 up to 521 seeds per

panicle, the last number on a plant of strain *121*. Of the entire number of plants 23, or 19 %, failed to give any seed at all and 58, or 47,9 % of the rest, produced less than 10 seeds per panicle. The strains that yielded the lowest average were *Kämpe* and the *Russian timothy*, while strain *121* heads the list with 44 seeds per panicle. This last-mentioned strain, as also appears from the notes made after the isolation tests in 1925 and 1926, seems to contain more »self-fertile» types than *Kämpe*. The few plants of *Gloria* and *Finnish timothy* examined indicate that these strains also give a better seed setting after isolation than *Kämpe*, strain *397* and the *Russian timothy*.

Of the plants isolated 70 were studied more closely in that the length of the different panicles was measured and the seed setting computed per cm. of the panicle. The seed setting of these plants amounted on the average to 1,4 seed per cm. The highest figure is 13,8 seed per panicle cm., produced by a plant of the *Finnish timothy*, which yielded 107,7 seed per panicle. Unfortunately only a few plants of strain *121* were tested in respect of length of panicle. The most »self-fertile» plant in this strain, however, with a yield of 521 seeds per panicle can be calculated, on the basis of the length of an average panicle, to give a seed setting of about 67 seeds per panicle cm., which represents a rather high degree of »self-fertility». From countings made on 6 panicles of varying lengths the number of florets per panicle cm. was estimated at about 145 and thus the said plant can be computed to yield approximately 46 % seed in the number of florets.

From the figures given it seems evident that varying degrees of »self-fertility» occur in different individuals and in different strains, hence it may be assumed that hereditary differences exist. In order to investigate a little more closely how matters stand in this respect a complete analysis of variance was made on the numerical material available. The results of this analysis are given in Table 17. In this table the strains *Kämpe* and *121* are grouped according to the different generations of inbreeding, *Kämpe* into I_0, I_2 and I_3 and strain *121* into I_1 and I_2 so as to make a comparison possible between material with varying degrees of inbreeding. As the basic figures for the analysis consisted of the number of seed per panicle the variation in a number of instances is very great and this is especially the case in plants with a relatively high degree of seed setting. The greatest variation within the plants was obtained in *Gloria*, which is however due to the fact that in plants with a good seed yield there also occurred single panicles which produced no seed, which is no doubt due to some unobserved

TABLE 17. *Analysis of Variance of the Seed Setting on Isolation in Different Strains of Timothy in 1927.*

	Average seed per panicle	Number of plants	Σd^2	D. F.	Variance
Kämpe					
I_0	11,3	5	—	—	—
Within plants	—	—	6945,72	55	126,29
Between »	—	—	4533,48	4	1133,37
Total	—	—	11479,20	59	194,56
I_2	2,1	10	—	—	—
Within plants	—	—	1540,93	107	14,40
Between »	—	—	1096,68	9	121,85
Total	—	—	2637,61	116	22,74
I_3	0,2	18	—	—	—
Within plants	—	—	48,78	189	0,26
Between »	—	—	62,88	17	3,70
Total	—	—	111,66	206	0,54
Entire Kämpe material	2,4	33	—	—	—
Within I_0, I_2 and I_3	—	—	14228,47	381	37,35
Between I_0, I_2 and I_3	—	—	5765,01	2	2882,52
Total	—	—	19993,48	383	52,20
Gloria I_0	35,7	9	—	—	—
Within plants	—	—	1925260,28	96	20054,77
Between »	—	—	195295,89	8	24411,98
Total	—	—	2120556,17	104	20389,98
Strain No. 397, I_1	13,4	13	—	—	—
Within plants	—	—	14105,04	143	98,64
Between »	—	—	51406,56	12	4283,88
Total	—	—	65511,60	155	422,66
Strain No. 121					
I_1	27,0	3	—	—	—
Within plants	—	—	5299,72	33	160,60
Between »	—	—	163260,00	2	81630,00
Total	—	—	168559,72	35	4815,97
I_2	45,0	54	—	—	—
Within plants	—	—	295698,59	549	538,61
Between »	—	—	4473827,28	53	84411,83
Total	—	—	4769525,87	602	7922,80
Entire material of strain 121	44,0	57	—	—	—
Within I_1 and I_2	—	—	4938085,59	637	7752,09
Between I_1 and I_2	—	—	11007,00	1	11007,00
Total	—	—	4949092,59	638	7757,19
Finnish timothy	36,3	5	—	—	—
Within plants	—	—	141410,20	55	2571,09
Between »	—	—	83411,76	4	20852,94
Total	—	—	224821,96	59	3810,54

	Average seed per panicle	Number of plants	Σd^2	D. F.	Variance
Russian timothy	1,3	4	—	—	—
Within plants	—	—	117,52	44	2,67
Between »	—	—	45,48	3	15,16
Total	—	—	163,00	47	3,47
All the strains	27,3	121	—	—	—
Within the strains	—	—	7296681,56	1379	5291,28
Between » »	—	—	491152,11	5	98230,42
Total	—	—	7787833,67	1384	5627,05

injury. The intraplant variation in *Gloria* will therefore be practically as great as the interplant variation, and therefore no significant difference in seed setting can be shown between the plants. In the other strains the interplant variation is significantly greater than the intraplant variation.

The *Kämpe* material, which consists of I_0, I_2 and I_3 plants, shows significantly different means for these three series. As the highest mean is obtained in I_0 and the lowest in I_3 this seems to indicate that an increased inbreeding brings about a loss of »self-fertility». The number of plants in each inbred generation is, however, too small to warrant any definite conclusions. As the different generations are not derived direct from one another then the lower seed setting of I_2 and I_3 need not be due to the degree of inbreeding, but may be explained as being due to the incidental selection of plants with a low degree of »self-fertility».

In strain *121* significantly divergent means were also obtained in both the inbred generations, but here the highest degree of »self-fertility» is found to be in the most inbred material. For the same reason as that given for *Kämpe* no positive inference can be drawn with reference to the effect of the degree of inbreeding on the seed setting. Strain *121*, however, seems to consist of a population with a comparatively high degree of »self-fertility», no matter in what inbred generation the isolations are made. I_3 plants of *Kämpe* (I_0) are derived from the isolations performed in 1925 on strain *404* (I_2), which has already been mentioned as being highly »self-sterile».

That the strains examined are populations with varying degrees of »self-fertility» is seen at the bottom of Table 17. The separate families show great divergencies from the total mean of 27,3 seed per

panicle. The inter-strain variation is also significantly greater than the total intra-strain variation.

General fertility. — In conjunction with the tests on »self-fertility» investigations were also made on the general fertility after free flowering of a number of the plants isolated in 1927. Thus, the length of panicle was measured and the number of developed seed counted in 6 panicles on each of 20 plants belonging to *Kämpe*, strain *121*, *Gloria*,

TABLE 18. *Seed Setting in Isolated and Free Panicles of Timothy in 1927.*

Plant No.	Strain	Isolated panicles			Free panicles			
		Number		Variance	Number			Variance
		Panicles	Seed per panicle		Panicles	Seed per panicle	Seed per cm panicle length	
4602	Kämpe ...	12	0	0	6	0	0	0
4611	» ...	12	0	0	6	0	0	0
4621	» ...	12	0	0	6	99,8	8,7	12,12
4694	» ...	12	0,2	1,68	6	172,8	21,9	269,88
4703	» ...	12	3,3	72,68	6	195,0	19,1	31,77
4625	Strain 121	9	6,0	96,00	6	289,2	22,6	281,91
4626	» »	9	70,3	6298,01	6	551,8	74,9	1661,00
4628	» »	12	5,6	243,12	6	256,3	33,1	2052,14
4629	» »	12	57,7	2637,00	6	395,2	38,4	238,14
4630	» »	9	10,5	804,25	6	223,2	22,2	380,36
4634	» »	12	163,4	49706,12	6	540,0	66,4	166,04
4635	» »	12	50,5	5853,00	6	345,8	46,4	276,95
4639	» »	9	0	0	6	296,5	26,0	96,30
4643	» »	12	9,5	97,00	6	118,2	13,4	247,79
4660	» »	6	32,0	6624,00	6	181,0	20,8	345,32
4664	» »	12	0,3	2,28	6	67,5	7,9	83,20
4674	» »	12	0,3	2,68	5	68,6	10,5	126,63
4686	Gloria	12	8,1	352,92	6	362,3	37,2	1156,12
4733	Russian ...	12	0,8	5,68	6	348,7	24,6	2429,54
4722	Strain 397	12	4,5	67,00	6	304,7	36,8	1898,24

Russian timothy and strain *397*. The results of this examination are tabulated in Table 18, which also gives the seed setting of the same plants in isolation. Two of the »self-sterile» plants were also sterile after free flowering, hence it may be assumed that these plants were female sterile. The matter was not subjected, however, to a close study. The other plants varied greatly in their capability of setting seed, ranging from 67,5 seed per panicle (7,9 seed per cm. of panicle) to 551,8 seed per panicle (74,9 seed per cm. of panicle). The highest result is

approximately equal to 52 % of the number of florets (cp. above p. 43). Thus, the plant giving seed in 46 % of the florets in isolation might be regarded as fully self-fertile. In computing the mean of the seed setting found in free inflorescences the two sterile plants were not included, because they may be looked upon as pure male plants (cp. WITTE 1919 b). The mean of the remaining 18 plants amounts to 261,4 seed per panicle, or 29,5 seed per panicle cm. The average obtained for these plants after isolation was not more than 24,0 seed per panicle, which is only 9,2 % of the seed set in free flowering.

The summarizing analysis of variance given in Table 19 shows that the total variation in both »self-fertility» and general fertility consists mainly of interplant variation, which is significantly greater than the intraplant variation.

TABLE 19. *Analysis of Variance of Seed Setting in Timothy in 1927.*

	Σd^2	D. F.	Variance
Isolations (18 plants)	—	—	—
Within plants	72863,42	180	404,80
Between »	332492,22	17	19558,37
Total	405355,64	197	2057,64
Free flowering (18 plants)	—	—	—
Within plants	11753,45	89	132,06
Between »	34487,61	17	2028,68
Total	46241,06	106	436,24

From Table 19 it appears further that the total variation in seed setting is considerably greater in isolated than in free panicles and this is true of both the intraplant variation and the interplant variation. In both cases there exist statistically significant differences.

Correlation between »self-fertility» and general fertility. — As Table 18 seemed to suggest that there existed a certain parallelism between »self-fertility» and general fertility the correlation between them was computed in the 18 plants where both were determined. A positive correlation, $r = + 0{,}7212$, was found, which has a great statistical significance, and we are therefore justified in drawing the conclusion that a correlation exists between seed setting in isolated and in free inflorescences under the conditions prevailing in this investigation. The analysis of variance of the seed setting in enclosed inflorescences is as follows: —

	Σd^2	D. F.	Variance
Total interplant	322492,22	17	19558,37
Regression upon general fertility ..	193874,46	1	193874,46
Remaining interplant	12816,76	16	8038,61
Intraplant	72863,42	180	404,80

The remaining interclass is significantly greater than the intraclass. Different environmental conditions of the plants can hardly have such a great modifying influence upon the isolation fertility as to account for the difference between intraplant and »remaining interplant» variance. Therefore, the great remaining interplant variance

TABLE 20. *Analysis of Variance of the Panicle Length of Isolated Timothy Plants in 1927.*

	Number		Average length mm.	Intraclass			Interclass		
	Panicles	Plants		Σd^2	D. F.	σ^2	Σd^2	D. F.	σ^2
Kämpe	231	20	83	27959	211	132,51	69264	19	3645,47
Strain 121.....	36	3	86	2820	33	85,45	7224	2	3612,00
Gloria.....	105	9	101	20151	96	209,91	16740	8	2092,50
Strain 397.....	156	13	108	17295	143	120,94	59124	12	4927,00
Finnish	60	5	90	5937	55	107,95	3492	4	873,00
Russian	48	4	95	9102	44	206,86	45660	3	15220,00
All the strains .	636	54	94	—	—	—	—	—	—
Total within strains	—	—	—	284768	630	452,01	—	—	—
Between strains	—	—	—	—	—	—	66984	5	13396,80

indicates a genetic variation in »self-fertility» which is independent of the general fertility.

Panicle length. — Simultaneously with the analysis of the fertility a measurement of the size of the panicles was obtained in the plants tested by measuring the length of the separate panicles. The average panicle lengths of the different strains are tabulated in Table 20. The shortest panicle is found in *Kämpe*, the average length of 20 plants being 83 mm., while in strain *397* the average length of the panicle in 13 plants is 108 mm. The total mean for all strains amounts to 94 mm. The means obtained cannot with certainty be considered representative for the strains as a whole but must be regarded only as the average of the individuals within the strains tested and these means can be proved to be significantly different. In each particular strain the variation in the length of the panicle is mainly an interplant variation, which is significantly greater than the intraplant variation.

Correlation between »self-fertility» and panicle length. — In order to obtain evidence as to whether the length of the panicles of different plants influences the »self-fertility» in any way the correlation coefficient was computed between the panicle length and the seed setting in isolation in the 54 plants tested in both respects. The result obtained, $r = + 0{,}0921$, does not indicate any correlation. This means then that in the material under examination the length of the panicle and the degree of »self-fertility» are independent characters which can be combined in various ways.

Experiments in 1928.

»Self-fertility». — In 1928 no isolations on a large scale were performed, only a few plants were subjected to some fertility tests. In various inbred families from strain *404* there appeared low, but profusely tillered and leafy individuals together with a few chlorophyll-deficient plants. 7 of these plants were isolated and the seed was also gathered after open pollination. All these plants failed to produce any seed in enclosed inflorescences and in open inflorescences only a few seeds per panicle were obtained. 5 plants derived from strain *121* were also isolated, 2 of which had white panicles and the other 3 had somewhat chlorophyll-deficient leaves. None of the plants were fully »self-sterile», but the seed setting of the different plants varied considerably. The plants with chlorophyll-deficient leaves produced on the average only 0,1 and 0,5 seed per panicle while the white panicled plants yielded an average of 0,2, 3,0 and 64,0 seed per panicle respectively.

Experiments in 1929.

»Self-fertility». — During the summer of 1929 breeding work was continued on the previously inbred material and a large number of new isolations were performed. Special attention was paid to strain *121*, partly because it had shown itself to be valuable from the standpoint of practical breeding and partly because the preceding year's tests had indicated that the most self-fertile types were found in this strain. In the plant material grown from the isolations made in 1926, comprising now, as far as strain *121* was concerned, an I_2 generation, a selection was made from 5 families, 5 plants of different types being chosen from each family. From the I_3 families of the same strain, which had been raised from I_2 plants isolated in 1927, a new selection of 42 plants was made from 6 different families, the number selected

from each family varying somewhat in accordance with the occurrence of valuable breeding types in the different families. Further, 5 plants of an I_3 family of *Kämpe* were isolated, and also 13 plants in three I_3 families of the *Finnish timothy*. In addition, 10 plants were isolated in a timothy population grown from a *Russian* seed-sample, which contained both the ordinary tall type of timothy and the low, prostrate *nodosum*-type. 5 of the mother plants isolated in 1927 were isolated as controls, the following numbers of seed per panicle being obtained: —

1927	17,8	57,7	149,0	4,2	26,6
1929	109,0	184,7	138,0	3,1	6,3

Coefficient of correlation + 0,58.

Control isolations of 9 plants isolated in 1928 gave the following result: —

1928	0	0	0	0	0	0	0	0,1	0,5
1929	0	3,8	0	0	0	0	0	0,1	5,2

As seen the agreement is fairly good, especially if we bear in mind that the »self-fertility» is given as the number of seed per panicle, which is of course not the best measure of the degree of seed setting.

Of the 10 plants isolated in the *Russian timothy* 5 were of the *nodosum*-type, while the remaining 5 belonged to the ordinary, tall type of timothy. The results of the fertility tests will be found in Table 21, from which it appears that the *nodosum*-plants are on the whole »self-sterile», only one of the plants examined giving one seed in 5 panicles. Even in free inflorescences these plants produce less seed than the tall type, and one of them was fully sterile, giving no seed in 10 investigated panicles. The tall plants of the »hay» or »semi-hay» type showed varying degrees of seed setting in isolation as well as in free flowering. The panicle is on the whole short. The results of my self-fertility tests agree very well with those obtained by SYLVÉN (1929) and JENKIN (1931 d) in isolations of *nodosum*-plants. The *nodosum*-forms of timothy thus seem to have in general a very low capacity of seed setting, but this does not exclude the possibility of there being found even among these types of timothy individual plants with a high degree of fertility, the truth of which is evidenced by one of the plants tested in the present material, which produced 54,3 seeds per panicle cm. in open pollination.

The results of the isolations performed in strains *121*, *Kämpe* and

Finnish timothy on previously inbred material are tabulated in Table 22 together with the degree of seed setting previously found in the mother plants. The mother plants in the 1926 isolations seem to transmit good and poor »self-fertility» to their progenies, in which nevertheless »self-sterile» and more or less »self-fertile» plants are found. In only 3 of the families are all the plants somewhat »self-fertile», but in the other families »self-sterile» types have also occurred. Although the small number of plants selected from each family cannot entirely cover the occurring variation we still get a clear picture of the differentiation in »self-fertility» between different plants. This is also the case in the progeny plants derived from the mother plants selected

TABLE 21. *Seed Setting and Panicle Length of Ten Russian Timothy Plants in 1929.*

	Isolations		Free flowering		Panicle length average mm.
	Number of seed per		Number of seed per		
	panicle	pan. cm.	panicle	pan. cm.	
Nodosum-type	0	0	117,3	20,8	56
»	0	0	20,0	3,3	61
»	0	0	315,0	54,3	58
»	0,2	0,07	23,7	3,9	61
»	0	0	0	0	17
Erect type	93,0	22,0	319,0	51,7	62
»	2,3	1,0	241,0	38,9	62
»	1,0	0,3	66,3	10,5	63
»	56,8	8,3	534,3	74,6	72
»	11,0	1,5	674,3	98,2	69

in 1927. Strain *121* shows in these families, as well as in those derived from the 1926 isolations, an intense variation in seed setting between the plants as well as between the families. Only 1 family, in which 2 plants were tested, is fully »self-sterile». The mother plant of this family also had a very low degree of »self-fertility», the yield in 1927 being not more than 0,1 seed per panicle. The only family representing *Kämpe* is fully »self-sterile». Of the 3 families of *Finnish timothy* one shows relatively good seed setting while the other two are fully »self-sterile».

On the whole, the agreement between the »self-fertility» of the mother plant and that of its progeny seems to be good, but the material is too small to warrant any definite judgment being made on this point, especially as the 1926 mother plants were not tested accurately.

Still, it is quite obvious that a differentiation has taken place, and in order to throw further light on this point a complete analysis of variance is given in Tables 23 and 24 of the seed setting in those 4 families in which all the plants have shown some seed setting. From Table 23 it will be seen that the interplant variation in »self-fertility» in each of these families is significantly greater than the intraplant variation. It may be further inferred from Table 24 that the inter-family variation is significantly greater than the intra-family variation.

TABLE 22. *Seed Setting of Mother Plants and Progeny. Comparison of the Number of Seeds per Isolated Panicle.*

Mother plants		Progeny		The seed setting of single progeny plants isolated in 1929							
No.	Seed setting	No.	Average seed setting	1	2	3	4	5	6	7	8
1745	good	3778	8,8	20,0	10,7	10,3	2,0	1,0	—	—	—
1746	weak	3783	3,7	18,0	0,3	0	0	0	—	—	—
1747	good	3785	50,1	146,3	57,0	31,0	11,7	4,3	—	—	—
1748	fairly good	3787	3,5	15,7	2,0	0	0	0	—	—	—
1759	fairly good	3810	3,9	11,0	6,7	2,0	0	0	—	—	—
1761	weak	3814	4,9	24,3	0	0	0	0	—	—	—
1763	fairly good	3819	20,9	47,0	44,3	6,7	4,0	2,7	—	—	—
4648	149,0	4874	2,6	18,0	0	0	0	0	0	0	—
4649	24,1	4876	22,1	162,3	14,3	0,1	0	0	0	0	0
4651	127,2	4880	15,7	73,3	0	0	0	0	—	—	—
4652	102,7	4882	12,5	67,8	2,7	0,3	0	0	0	—	—
4653	17,3	4884	1,8	6,7	1,3	1,0	0	0	—	—	—
4668	0,1	4911	0	0	—	—	—	—	—	—	—
4696	10,5	4962	0	0	0	0	0	0	—	—	—
4708	31,7	4985	0	0	0	0	0	0	—	—	—
4709	29,4	4987	48,9	90,0	40,0	16,7	—	—	—	—	—
4711	7,5	4990	0	0	0	0	0	0	—	—	—

General fertility. — All isolated plants have also been examined with respect to fertility in free flowering, and even these tests show that there is a great variation in the seed setting of different plants. Not less than 8 produced no seed at all, this being confirmed by an examination of all the developed panicles on these plants. These were of course also self-sterile. In these instances we can suspect the existence of female sterility. Other plants varied greatly, the largest number of seed set being 1246,3 seed per panicle, or 145,5 seed per panicle cm., by a plant of strain *121*. From Tables 23 and 24 it is seen that the interplant variation is significantly greater than the intraplant

TABLE 23. *Analysis of Variance of Seed Setting in Isolated and Free Panicles of the Families 3778, 3785, 3819 and 4987 in the Year 1929.*

	3778			3785			3819			4987		
	Σd^2	D. F.	Variance	Σd^2	D. F.	Variance	Σd^2	D. F.	Variance	Σd^2	D. F.	Variance
Isolation												
Within plants	3,57	10	0,36	179,30	10	17,93	10,21	10	1,02	19,90	6	3,32
Between »	33,37	4	8,34	583,35	4	145,84	90,69	4	22,67	216,74	2	108,37
Total	36,94	14	2,64	762,65	14	54,48	100,90	14	7,21	236,64	8	29,58
Free flowering												
Within plants	3059,25	10	305,92	643,54	10	64,35	2032,10	10	203,21	413,64	6	68,94
Between »	11001,26	4	2750,31	2852,89	4	713,22	8761,71	4	2190,43	1052,37	2	526,18
Total	14060,50	14	1004,32	3496,43	14	249,74	10793,82	14	770,99	1466,01	8	183,25

variation. The differences in seed setting between the families are also significant.

Correlation between »self-fertility» and general fertility. — As a considerable differentiation could also be ascertained in the general fertility it might be of interest to find out to what an extent seed setting in enclosed and in open inflorescences are correlated with each other. The correlations in the 4 families analysed more closely are: —

Family No.	Number of Pairs	*r*
3778	5	+ 0,6281
3785	5	+ 0,3321
3819	5	+ 0,7592
4987	3	+ 0,3189

TABLE 24. *Summarizing Analysis of Variance of Seed Setting in the Families 3778, 3785, 3819 and 4987 in the Year 1929.*

	Σd^2	D. F.	Variance
Isolation			
Within plants within families	212,98	36	5,92
Between plants within families	724,16	14	51,73
Total within families	937,14	50	18,74
Between families	405,11	3	135,04
Total	1342,25	53	25,33
Free flowering			
Within plants within families	6148,52	36	170,79
Between plants within families	23668,22	14	1690,59
Total within families	29816,74	50	596,34
Between families	42767,32	3	14255,77
Total	72584,06	53	1369,51

There thus seems to exist a positive correlation but it cannot be shown to have any statistical significance within the separate families. The only family in which it can be assumed with any degree of probability that a correlation really exists is No. 3819. As no significant divergencies can be shown between the correlations obtained a total correlation has been computed for the whole of the material tested, altogether 98 plants. Then we obtain $r = + 0{,}4125$, which has a great statistical significance ($P > 99 : 1$), and we can therefore consider it proved that the variations in »self-fertility» and general fertility are to a great extent dependent on each other.

The analysis of variance of the »self-fertility» between the plants is as follows: —

	Σd^2	D. F.	Variance
Total interplant	17192,17	97	177,21
Regression upon general fertility	2985,00	1	2985,00
Remaining interplant	14207,13	96	147,99

Experiments in 1930.

»*Self-fertility*». — All plants in one very variable I_1 family of *Kämpe* were vegetatively propagated in the autumn of 1929. Isolations were made on all clones in 1930, two plantlets in each clone having three panicles bagged together. Further, renewed isolations were performed on the 9 plants of the two strains *Kämpe* and *121* investigated in 1928 and 1929. Five *nodosum*-like plants of the *Russian timothy* were also isolated, but these plants were not so prostrate as those isolated in 1929.

Moreover, a new selection of mother plants was made from the same material as in 1929, but this time only the most vigorous individuals in a number of families were chosen. From some of these families 3 or 4 plants were selected, from others only 1, but as a rule 2 mother plants were selected from each family.

In quite new material, transplanted from localities in the South of Sweden, isolations were made on 14 plants of various types of timothy, 5 of them being of *nodosum*-type from the Island of Öland.

Altogether 130 plants were isolated, which will be treated in different series according to their derivation and type. No examination of seed setting after free flowering was possible until late in the autumn, but by that time much of the seed had fallen out of quite a number of the panicles and therefore no accurate examination could be made.

The control isolations on the 9 fully, or almost fully, »self-sterile» plants examined in 1928 and 1929 even this year showed results of seed setting entirely in accord with those obtained in the two previous years. 5 of the plants failed to give any seed at all while the others yielded very few seeds.

The new isolations in the *Russian timothy* yielded a better result than was obtained from the plants examined in 1929. Thus, none of the plants selected were quite »self-sterile» although the number of seed set was low. The average yield per plant was 3,0, 3,7, 5,8, 7,0 and 20,7 seeds per panicle.

The new material collected, which can be considered free from previous inbreeding, also showed a very varying yield of seed in the different plants. 4 of the 5 *nodosum*-plants from Öland were fully »self-sterile» while the 5th gave only 1 seed in the 6 panicles isolated. The other 9 wild plants (erect type), 4 of which had also been collected on the Island of Öland, gave a yield ranging from 0,5 to 22,0 seed per panicle. Even from these figures we might be justified in saying that types having different degrees of »self-fertility» have been met with even in wild growing material. From the analysis of variance confirmation was obtained that they are to be regarded as having varying degrees of »self-fertility».

TABLE 25. *Number of Isolated Plants in Different Timothy Strains in the Year 1930.*

Strain	Inbreeding generation	Number		Average seed per panicle
		Families	Plants	
Kämpe	I_1	1	1	0
»	I_3	1	1	45,4
»	I_4	1	1	0
121	I_2	2	7	18,4
»	I_3	17	28	65,3
Gloria	I_1	4	6	3,0
Finnish	I_3	2	5	52,2
397	I_2	1	2	23,3
Total		29	51	45,7

The new selection of mother plants from the previously inbred material consisted of 51 plants, distributed among different strains as shown in Table 25. The different plants show quite different degrees of seed setting. The differentiation between the families derived from the different mother plants seems to be very great. The means of the different inbred generations of the strains examined are given in Table 25, from which it will be seen that the highest mean is obtained in the I_3 generation of Strain *121*. The total mean of all plants reaches 45,7 seeds per panicle. It is interesting to note that the I_3 plant of *Kämpe* selected yielded a relatively large number of seeds, which proves that even in this strain individuals with a comparatively high degree of self-fertility can be met with, although not so frequently as in some other strains. Of the particular plants tested 5 of them

were »self-sterile», of which 2 belonged to *Kämpe*, 2 to strain *121* and 1 to *Finnish timothy*.

The highest yield was 313,7 seed per panicle (31,8 per panicle cm.) by an I_3 plant of strain *121*. In another I_3 family of the same strain 4 plants examined gave 293,8, 230,7, 155,5 and 195,3 seeds per panicle respectively, which indicates that this family consisted mainly of types with a relatively high degree of self-fertility. In comparing these plants with the mother plant of the family, which showed a yield of 306,1

TABLE 26. *Analysis of Variance of Seed Setting in Isolated Timothy Plants in 1930, Compared with the Seed Setting in the Mother Plants Isolated in the Year 1927.*

Mother plant		Progeny family			Intraplant			Interplant		
No.	Seed per panicle	No.	Average seed per panicle	Number of plants	Σd^2	D. F.	σ^2	$\Sigma(nD^2)$	D. F.	σ^2
4630	10,5	4840	92,7	2	1125,34	4	281,34	294,00	1	294,00
4631	1,2	4842	1,5	2	11,70	10	1,17	21,90	1	21,90
4635	50,5	4849	13,4	2	718,94	10	71,89	483,90	1	483,90
4641	2,3	4860	5,0	2	160,68	10	16,07	34,68	1	34,68
4645	52,7	4868	33,5	2	1138,00	9	126,44	12344,75	1	12344,75
4649	24,1	4876	128,4	2	35154,54	10	3515,45	87313,08	1	87313,08
4651	127,2	4880	3,5	3	81,52	15	5,43	139,02	2	69,51
4676	306,1	4925	218,8	4	105605,00	20	5280,25	61954,50	3	20651,50
4688	22,6	4948	4,8	2	210,18	10	21,02	10,86	1	10,86
4692	67,2	4956	2,2	2	43,20	9	4,80	7,04	1	7,04
4705	4,1	4980	3,0	4	14148,68	20	707,43	2311,08	3	770,36
4707	77,0	4983	32,6	3	3927,22	15	261,81	11008,02	2	5504,01
4709	29,4	4987	65,3	4	35301,04	20	1765,05	44131,38	3	14710,46
4716	8,3	4999	23,3	2	1078,50	10	107,85	1399,68	1	1399,68
4729	12,2	5022	45,4	2	1269,34	10	126,93	343,50	1	343,50

seed per panicle in 1927, we find the parallelism between the »self-fertility» of the mother plant and that of the progeny so manifest that we can assume a nearly constant high degree of »self-fertility». A glance at Table 26 will show that even the other mother plants have transmitted their »self-fertility» to their progenies. In this Table the degrees of seed setting in the mother plants have been tabulated together with the mean seed setting of the progeny of those families from which at least 2 individuals were tested in 1930. The parallelism is, on the whole, very obvious, as will appear also from the correlation coefficient, which is $r = +0{,}4507$ in the entire material (29 pairs). There is sufficient statistical significance in this number of pairs (the probability is

more than 99 : 1) to show that a correlation really exists and therefore it can be considered as proved that unequal degrees of self-fertility are transmitted to the progeny. That the correlation is not greater must be considered as due to the small number of progeny plants tested, and also to the fact that different years may modify the self-fertility in varying degrees. Even judged by the averages the parallelism is however striking, for the mean of the mother plants tested in 1927 was 46,5 seeds per panicle and the mean of the seed setting of the progeny plants of these mother plants examined in 1930 was 45,7 seeds per panicle.

TABLE 27. *Summarizing Analysis of Variance of Seed Setting in Timothy Isolations in the Year 1930.*

	Σd^2	D. F.	Variance
Within plants within families	199973,88	182	1098,76
Between plants within families	221797,39	23	9643,36
Total within families	421771,27	205	2057,42
Between families	359391,41	14	25670,81
Total	781162,68	219	3566,95

The analysis of variance of the »self-fertility» in 1930 (Table 26) shows that the interplant variation is in almost every instance greater than the intraplant variation, even if the differences are not always statistically significant. From Table 27 it will be seen that in the whole of the material the interplant variance is decidedly greater than the intraplant variance, there being no doubt that this is not due to chance. Therefore, it can be proved that on the average the differentiation between the plants is obvious, even if this cannot be shown within every single family, partly because the number of plants examined was too small and partly because certain families show a relative constancy in »self-fertility». From Table 26 we further see that the families are highly differentiated with respect to »self-fertility».

The intensely segregating I_1 family, No. 4933, from *Kämpe* also showed a great variation in »self-fertility». The mother plant of this family, No. 4680, produced an average of 14,5 seeds per panicle in 12 isolated panicles in 1927, and renewed isolations in 1930 gave 26,7 seeds per panicle, or 2,7 seeds per panicle cm., in an average of 6 panicles. All the I_1 plants were vegetatively propagated in the autumn of 1929. Some of the clones died out in the following winter. Of

those still living 4 were very weak and had small stunted panicles, from which the florets fell off at flowering time, leaving only the bare rachis. These clones were absolutely sterile and were not isolated. 64 clones had normally developed panicles, although they differed in size and appearance. These were isolated in 1930. As was to be expected from the more or less vigorous appearance of the clones they differed very much in the degree of seed setting. 15 of them were fully »self-sterile» while the others showed a higher or lower degree of »self-fertility» up to 38,7 seeds per panicle cm. (112 seeds per panicle).

TABLE 28. *Summarizing Analysis of Variance of the Seed Setting in Isolations of the Family 4933 from Kämpe. Isolations in 1930.*

	Σd^2	D. F.	Variance
Between panicles within isolations within clones	1321,65	248	5,33
Between isolations within clones	1021,43	64	15,96
Total within clones	2343,08	312	7,51
Between clones	23832,20	63	378,29
Total	26175,28	375	69,80

The distribution of the variants into different classes of self-fertility was as follows: —

Number of seed per panicle cm.	0	0,1—1	1—2	2—3	3—4	4—5	5—6	6—7	7—8
Number of clones	15	11	5	2	5	4	4	1	2

8—9	9—10	10—11	11—12	12—13	13—14	14—15	15—16	16—17	17—18	18—19	19—20	20—30	30—40
1	2	4	1	1	1	1	1	—	—	—	—	2	2

There is an even distribution in different gradations with an evident maximum only in the 0-class and the lowest fertility class. Although the modifications may of course easily shift the »actual» figures from one class to another in this limited classification it still seems evident that a differentiation into different gradations has taken place. This is still more evident from the analysis of variance given in Table 28. From this it will be seen 1) that the inter-isolation variance (between different isolated plantlets within the same clone) is greater than the intra-isolation variance (between the panicles within the same isolation) and 2) that the inter-clone variance is greater than the intra-clone variance. In both cases the difference is of great statistical significance. This implies that the modifications affect different isolations to a

greater extent than different panicles enclosed in the same isolating bag and it also implies that there exists an intense variation between the clones.

However, there is such a great variation in this family with respect to other characters that its self-fertility must be looked upon in connection with the vigour of the plants, a matter that will be treated in the next chapter. But even here it may be pointed out that on the average seed setting is not lower in the progeny than in the mother plant, for in 1930 the »self-fertility» of the mother plant was found to be 2,7 seed per panicle cm. while the average yield of the progeny was 5,3 seed per panicle cm.

b) THE EFFECT OF SELF-FERTILIZATION ON THE PROGENY.

The investigations carried out in relation to the effect of inbreeding in timothy were made on the same material as that dealt with in connection with the analyses of fertility.

Of the investigations made into the variation in different characters in families after isolation and after free flowering an account has already been given concerning the tests on fertility. Moreover, the material as a whole has been chiefly analysed carefully with respect to the variation in height, but some families have also been examined regarding other characters.

Progenies after mother plants selected in 1925.

The material raised from the isolations performed in 1925 was not subjected to a close examination. As no seed had been harvested from the open inflorescences of the mother plants no comparisons were possible between inbred and »outbred» progenies. As the »self-fertility» of the majority of the mother plants was low their subsequent progenies were very few in number, which rendered it difficult to form any reliable opinion of the variability of the different characters. The *I* families of strain *121* are characterised in general by being on the average taller, less profusely tillered and having a more gracile type of growth than the *I* families of strain *404*, which were as a rule lower and in some cases with very profuse tillering. The variation between the different families of strain *121* was very great, which indicates that different types had been separated by self-fertilization. The *I* families of strain *404* were more similar in their morphological characters, even if in some cases differentiation seemed to have taken

place. As already mentioned, there appeared a number of plants in strain *404* which were low in stature but otherwise vigorously developed, and in strain *121* one family was noted with 2 plants having albino panicles and another two families with some plants having chlorophyll-deficient leaves.

Progenies after mother plants selected in 1926 and 1927.

Defective plants. — The progenies of the mother plants selected in 1926 and 1927 were studied extensively in families after isolation and after open pollination. A more or less intense variation in different characters appeared in both *I* and *K* families. After the 1926 isolations 2 albino plants appeared in an I_2 family of strain *121*. In other respects these plants were vigorous and normally developed. A few solitary chlorophyll variants were also noted in a great many *I* families but no definite figures were obtainable. These chlorophyll-deficient individuals occurred in greatly varying proportions in the different families, not only in *I* families but also in *K* families as well. A great number of different types with unequal degrees of chlorophyll development were observed, ranging from pure albino to pure green with transitions to striated types of varying intensity as well as yellow and yellowish green individuals. That the segregation varied in different families is manifest and several genetic factors seem to occur.

The occurrence here and there of single individuals without any fertile straws is also interpreted as a recessive product of segregation. In various families an intense differentiation seems to have taken place in immunity against rust, in tillering, leafiness, length of panicle and several other properties.

Winter hardiness. — Even with respect to winter hardiness manifest differences could be observed in 1929 between the families, *I* families as well as *K* families. In an aggregate of 30 *I* families derived from the 1926 mother plants the average mortality was 15,5 %, while the corresponding *K* families showed an average mortality of only 1,6 %. On examining the separate groups of *I* and *K* families it will be found that in 4 cases the mortality is highest in the *K* families, in 6 cases it is equal in *I* and *K* families while in 29 groups the *I* families show a greater percentage of dead plants than the corresponding *K* families. These results plainly indicate that winter hardiness is on the average lower in the *I* material than in the *K* material.

The variation in mortality between the inbred families has

TABLE 29. *Analysis of Variance of the Height of Inbreeding Material in Timothy. Isolations in 1926. Measurements in 1929.*

Group No.	Family No.	Basic population	Inbreeding generation	Number of plants	Average height cm.	Variance	Group average cm.	$Var._t$	$Var._{ab}$	$Var._p$
1	3739	Common commercial strain	K	109	109	44,75	108	51,60	46,84	609,00
	40	»	I_1	20	103	58,74				
2	41	»	K	100	101	71,32	94	89,60	63,60	5733,00
	42	»	I_1	117	87	56,00				
3	43	»	K	120	103	46,39	103	52,77	51,95	108,00
	44	»	I_1	12	100	112,09				
4	47	»	K	120	103	77,03	100	81,07	72,04	2160,00
	48	»	I_1	120	97	67,04				
5	49	»	K	39	112	40,05	114	48,74	42,32	488,00
	50	»	I_1	38	117	44,70				
6	51	»	K	39	105	84,34	101	122,12	110,89	975,00
	52	»	I_1	39	98	137,45				
7	53	»	K	40	105	37,44	98	74,80	25,50	3920,00
	54	»	I_1	40	91	39,21				
8	57	»	K	120	113	53,13	105	118,14	54,10	15360,00
	58	»	I_1	120	97	55,07				
9	59	»	K	20	113	51,37	109	96,03	72,88	860,00
	60	»	I_1	15	103	102,07				
10	61	»	K	40	107	56,31	103	80,08	68,06	946,00
	62	»	I_1	34	100	81,94				
11	77	Strain 121 I_1	K	120	106	72,54	99	121,00	72,10	11662,00
	78	» » »	I_2	118	92	71,64				
12	82	» » »	K	119	100	57,07	97	96,32	84,84	2719,00
	83	» » »	I_2	103	93	116,96				
13	84	» » »	K	118	106	55,13	102	78,11	57,73	4888,00
	85	» » »	I_2	120	97	60,29				
14	86	» » »	K	120	106	129,36	101	155,22	130,00	5850,00
	87	» » »	I_2	114	96	130,67				
15	96	» » »	K	120	97	84,93	89	188,72	116,51	17157,00
	97	» » »	I_2	117	80	148,91				
16	3809	» » »	K	120	102	89,22	99	101,33	89,16	2984,00
	10	» » »	I_2	119	95	89,03				
17	11	» » »	K	79	109	44,26	102	114,06	65,17	7399,00
	12	» » »	I_2	72	95	88,14				
18	13	» » »	K	60	94	81,14	81	299,68	117,32	20724,00
	14	» » »	I_2	54	67	157,60				
19	15	» » »	K	120	103	102,84	100	104,82	96,21	2034,00
	16	» » »	I_2	106	97	88,69				
20	18	» » »	K	120	99	62,54	92	134,88	78,54	13432,00
	19	» » »	I_2	118	84	94,81				
21	22	» » »	K	40	104	70,54	101	96,80	85,52	920,00
	23	» » »	I_2	35	97	102,71				
22	37	Kämpe	K	118	110	61,56	112	76,72	74,54	591,00
	38	»	I_1	119	113	87,41				
23	41	»	K	40	99	80,46	96	96,77	73,65	1160,00
	42	»	I_1	8	86	35,71				
24	44	»	K	39	116	73,89	116	72,60	74,21	5,00
	45	»	I_1	5	115	77,25				

Group No.	Family No.	Basic population	Inbreeding generation	Number of plants	Average height cm.	Variance	Group average cm.	Var_t	Var_{ab}	Var_p
25	3846	Kämpe	*K*	118	123	42,54	117	94,01	58,11	8568,00
	47	»	I_1	120	111	73,40				
26	50	»	*K*	58	107	90,89	101	169,86	128,11	4930,00
	51	»	I_1	58	94	165,32				
27	52	»	*K*	40	107	142,92	105	133,79	118,16	993,00
	53	»	I_1	17	98	57,81				
28	54	»	*K*	120	116	104,19	110	182,69	159,07	5733,00
	55	»	I_1	117	103	215,37				
29	56	»	*K*	120	114	106,21	110	99,61	83,90	3824,00
	57	»	I_1	119	106	61,40				
30	58	»	*K*	40	115	86,56	111	144,96	106,17	2240,00
	59	»	I_1	16	101	157,13				
31	60	»	*K*	40	109	44,74	109	44,32	45,13	0,00
	61	»	I_1	17	109	46,06				
32	62	Gloria	*K*	40	103	44,67	102	92,00	87,45	315,00
	63	»	I_1	11	97	254,30				
33	64	»	*K*	40	101	30,33	101	27,82	28,39	0,00
	65	»	I_1	11	101	20,80				
34	68	»	*K*	40	103	86,79	101	104,78	93,60	608,00
	69	»	I_1	7	93	137,83				
35	70	»	*K*	33	95	116,47	92	165,88	142,93	1107,00
	71	»	I_1	10	83	237,00				
36	74	»	*K*	31	98	105,30	98	109,65	111,44	40,00
	75	»	I_1	10	96	131,89				
37	76	»	*K*	34	98	44,36	95	123,79	92,78	1395,00
	77	»	I_1	9	84	292,50				
38	80	»	*K*	34	101	53,48	98	86,95	57,28	1274,00
	81	»	I_1	8	87	75,14				
39	82	»	*K*	108	91	61,48	83	109,54	52,99	12155,00
	83	»	I_1	107	76	46,75				

$\sigma^2 = 385{,}03$ and between the *K* families $\sigma^2 = 18{,}73$, which furnishes a statistically significant proof that the differentiation is greater between the *I* families than between the *K* families. The coefficient of correlation between the mortality in the *I* families and that in the corresponding *K* families gives $r = -0{,}1178$, which has no statistical significance.

In the material after the 1927 mother plants which survived only one winter, the mortality is lower, amounting on the average to 6,3 % in the *I* families and 0,7 % in the *K* families. Even in this material the average mortality is, as we see, considerably higher in the *I* material than in the *K* material. In 18 groups all the plants planted out were still living and in the other groups the rate of mortality is, with but one exception, higher in the *I* families than in the *K* families. The highest percentage of dead plants is 46,5, which occurred in an *I* family, whereas the highest figure for the *K* material is 6,9 %. It is

quite manifest that a greater differentiation in the duration of life has occurred in the *I* material than in the *K* material. Some families with a high rate mortality also show a relatively large number of chlorophyll-deficient individuals.

Height. — In the progenies from mother plants chosen in 1926 the variation in height was determined in 39 groups of *I* and *K* families. The averages for each family and the extent of the variation within each family, within each group and between the families within the groups are presented in Table 29. From this table it will be seen that the average heights are in general lower in the *I* families than in the *K* families.

The variances in the different families vary very much, being sometimes higher in the *I* family and sometimes higher in the *K* family of the same group. In the last three columns of Table 29 will be found the total variance within the group, var_t, the intra-family variance, var_{ab}, and the inter-family variance, var_p. All these variances are very variable within the different groups. In most groups var_p has a greater value than var_{ab} and therefore there is a greater variation between the families than within the families. In *Common commercial* this is the case in all groups and there is a statistical significance that the differences really exist in all but one group, group No. 3. In one of these groups the *I* family is taller than the *K* family but in the other groups the *I* family is lower. In group 3, where no significance exists for any real difference, the means of the *I* and *K* families cannot be shown to be unequal. In strain *121* all groups can be shown to be significantly differentiated, with different means for the *I* and the *K* families, the *I* families being generally lower. In the 10 groups of *Kämpe* examined the height cannot be shown to be significantly different in the *I* and *K* families of groups 24 and 31, in the other groups, however, the means of the *I* and *K* families are significantly different, the *I* family being lower in 7 groups and higher in one group, No. 22. In *Gloria* 5 of the groups exhibit significant differences in height between the *I* and *K* families, whereas in the remaining groups (Nos. 31, 33 and 36) no differentiation in height can be shown between the families.

In examining the variation of height in the material after the 1927 mother plants we find a similar state of affairs as in the material treated above. In Table 30 it will be seen that all groups of *Kämpe* — 5 with I_1 and 2 with I_3 families — show lower means in the *I* families than in the *K* families, but in one group, No. 7, this difference in height is without any significance. Of the groups tested in strain *121* three of them consisted of I_2 families and the others of I_3 families along with their corresponding *K* families. Two of the I_2 families are lower than the *K* families with significantly different means, the third (No. 9) is also somewhat lower than the *K* family, but the difference is too slight to have any significance. Of the groups comprising I_3 families one of them (No. 26) shows an insignificantly higher mean in the *I* family, in another group (No. 28) the means are the same in both families. In 4 of the groups (Nos. 18, 19, 24 and 29) the I_3 families are insignificantly lower than the *K* families. In 6 of the I_3 groups in this strain there is thus no certain differentiation between the *I* and the *K* families, while in the remaining 21 groups

TABLE 30. *Analysis of Variance of the Height of Inbreeding Material in Timothy. Isolations in 1927. Measurements in 1929.*

Group No.	Family No.	Basic population	Inbreeding generation	Number of plants	Height average cm.	Variance	Group average	Var_t	Var_{ab}	Var_p
1	4935	Kämpe	K	40	95	110,21	89	239,05	181,13	2440,00
	34	»	I_1	40	84	66,28				
2	37	»	K	40	103	83,23	99	120,34	77,89	2540,00
	36	»	I_1	19	89	66,33				
3	39	»	K	120	94	98,76	91	93,86	85,18	2151,00
	38	»	I_1	119	88	71,48				
4	41	»	K	40	103	103,44	99	151,41	87,64	3340,00
	40	»	I_1	12	84	31,64				
5	43	»	K	40	113	67,23	109	121,63	98,50	1648,00
	42	»	I_1	28	103	143,67				
6	63	»	K	38	117	156,57	113	255,48	150,84	4964,00
	62	»	I_3	9	91	110,56				
7	5023	»	K	39	121	49,63	121	57,59	57,99	31,00
	22	»	I_3	31	120	68,57				
8	4979	Strain 121	K	40	104	233,00	103	259,44	230,29	1484,00
	78	» »	I_2	4	84	195,00				
9	81	» »	K	40	108	73,13	109	58,42	58,74	40,00
	80	» »	I_2	20	109	29,21				
10	84	» »	K	100	105	70,97	100	70,90	59,96	2225,00
	83	» »	I_2	99	95	48,85				
11	4831	» »	K	40	124	162,05	120	204,93	183,06	1648,00
	30	» »	I_3	28	114	213,41				
12	33	» »	K	116	123	149,53	114	243,55	162,91	18549,00
	32	» »	I_3	113	105	176,64				
13	35	» »	K	139	124	117,29	118	151,66	115,98	9216,00
	34	» »	I_3	117	112	114,41				
14	37	» »	K	40	119	74,33	113	147,47	106,49	3057,00
	36	» »	I_3	33	106	145,69				
15	39	» »	K	120	121	203,85	115	229,48	188,09	9416,00
	38	» »	I_3	104	108	150,10				
16	41	» »	K	80	117	124,89	111	170,56	121,98	7360,00
	40	» »	I_3	70	103	118,65				
17	43	» »	K	40	124	77,67	121	153,13	129,57	1260,00
	42	» »	I_3	9	111	382,63				
18	45	» »	K	40	114	67,26	114	62,91	64,02	16,00
	44	» »	I_3	4	112	22,00				
19	48	» »	K	119	106	88,93	105	93,56	92,94	237,00
	47	» »	I_3	118	104	96,99				
20	50	» »	K	120	112	125,24	109	158,94	147,00	2952,00
	49	» »	I_3	117	105	169,44				
21	52	» »	K	79	110	89,67	108	94,90	91,48	612,00
	51	» »	I_3	74	106	93,41				
22	54	» »	K	60	117	77,63	113	115,82	92,14	2508,00
	53	» »	I_3	43	107	112,52				
23	59	» »	K	40	113	90,38	111	270,59	84,82	8630,00
	58	» »	I_3	7	100	48,67				
24	61	» »	K	32	103	77,16	102	104,55	102,02	208,00
	60	» »	I_3	11	98	179,10				

Group No.	Family No.	Basic population	Inbreeding generation	Number of plants	Height average cm.	Variance	Group average	$Var._t$	$Var._{ab}$	$Var._p$
25	4863	Strain 121	K	37	109	113,33	108	126,08	108,21	805,00
	62	» »	I_3	3	92	16,00				
26	65	» »	K	40	117	86,59	118	75,77	75,77	76,00
	64	» »	I_3	36	119	63,71				
27	67	» »	K	40	102	62,05	99	91,30	68,90	1256,00
	66	» »	I_3	14	91	89,46				
28	69	» »	K	117	99	123,33	99	145,16	145,85	0
	68	» »	I_3	95	99	173,64				
29	71	» »	K	40	103	86,13	103	119,86	120,90	76,00
	70	» »	I_3	4	100	573,00				
30	73	» »	K	100	109	56,52	101	147,83	91,51	11300,00
	72	» »	I_3	100	94	126,51				
31	75	» »	K	158	97	121,13	89	227,97	164,30	19712,00
	74	» »	I_3	150	81	209,78				
32	77	» »	K	58	98	143,84	88	295,59	156,58	13640,00
	76	» »	I_3	40	74	175,21				
33	79	» »	K	117	98	156,75	97	108,35	106,29	585,00
	78	» »	I_3	117	95	55,84				
34	81	» »	K	100	105	103,27	99	177,64	129,30	8976,00
	80	» »	I_3	84	91	160,35				
35	83	» »	K	149	93	255,62	90	241,86	231,24	2717,00
	82	» »	I_3	86	86	188,78				
36	85	» »	K	40	98	220,03	94	255,14	209,35	2499,00
	84	» »	I_3	11	81	167,70				
37	87	» »	K	39	96	141,08	93	133,70	126,31	666,00
	86	» »	I_3	35	90	109,79				
38	4945	Gloria	K	131	113	85,79	111	89,40	81,68	1612,00
	44	»	I_1	68	107	73,69				
39	47	»	K	39	99	118,26	98	98,05	96,18	201,00
	46	»	I_1	18	95	46,82				
40	49	»	K	119	104	104,53	107	108,64	102,56	1551,00
	48	»	I_1	120	109	100,60				
41	57	»	K	120	116	92,92	114	119,45	93,12	3989,00
	56	»	I_1	29	103	93,96				
42	86	Finnish	K	100	105	125,20	97	186,41	122,71	12800,00
	85	»	I_3	100	89	120,21				
43	88	»	K	40	111	52,03	108	51,99	43,44	711,00
	87	»	I_3	39	105	35,55				
44	91	»	K	40	102	100,69	96	167,03	114,23	3546,00
	90	»	I_3	26	87	135,36				
45	93	»	K	80	109	75,44	109	82,69	82,71	80,00
	92	»	I_3	80	110	89,97				
46	5039	Freja	K	79	118	72,56	116	94,94	88,97	1027,00
	38	»	I_1	79	113	105,37				
47	27	Primus	K	40	112	98,21	109	169,07	108,35	2780,00
	26	»	I_1	5	87	207,25				
48	31	Russian	K	40	121	111,21	120	97,36	98,00	60,00
	30	»	I_1	20	119	70,89				
49	35	»	K	40	110	62,46	103	95,61	53,24	3400,00
	34	»	I_1	40	97	44,03				

TABLE 31. *Summarizing Analysis of Variance of the Whole Timothy Material in 1929.*

	Number			Height average cm.	Σd^2	D. F.	Variance
	Plants	Families	Groups				
Isolations in 1926							
After free flowering. *K*...	2976	39	—	106	—	—	—
Within families	—	—	—	—	212665	2937	72,41
Between »	—	—	—	—	146670	38	3859,74
Total	—	—	—	—	359335	2975	120,78
After isolation. *I*.....	2400	39	—	95	—	—	—
Within families	—	—	—	—	224461	2361	95,07
Between »	—	—	—	—	256868	38	6759,68
Total	—	—	—	—	481329	2399	200,64
Isolations in 1927							
After free flowering. *K*...	3505	49	—	108	—	—	—
Within families	—	—	—	—	399600	3456	115,63
Between »	—	—	—	—	299276	48	6234,92
Total	—	—	—	—	698876	3504	199,45
After isolation. *I*.....	2628	49	—	99	—	—	—
Within families	—	—	—	—	310269	2579	120,31
Between »	—	—	—	—	290034	48	6042,38
Total	—	—	—	—	600303	2627	228,51
Isolations in 1926 and in 1927 together							
After free flowering. *K*...	6481	88	—	107	—	—	—
Within families	—	—	—	—	612265	6393	95,77
Between »	—	—	—	—	461799	87	5308,03
Total	—	—	—	—	1074064	6480	165,75
After isolation. *I*.....	5028	88	—	97	—	—	—
Within families	—	—	—	—	534730	4940	108,24
Between »	—	—	—	—	561519	87	6454,24
Total	—	—	—	—	1096249	5027	218,07
K- and *I*-families in groups.....	11509	176	88	103	—	—	—
Within families within groups.....	—	—	—	—	1146993	11333	101,28
Between fam. within groups.....	—	—	—	—	346463	88	3937,08
Total within groups ...	—	—	—	—	1493456	11421	130,76
Between groups	—	—	—	—	1005744	87	11560,28
Total	—	—	—	—	2499200	11508	217,17

a significant differentiation has taken place, resulting in lower means in the I_3 families than in the *K* families. The material in *Gloria* consists of 4 groups, 3 of which have significantly different means in the *I* and *K* families, two of them (38 and 41) having lower means in the *I* families and the third (No. 40) having a higher mean in the *I* family than in the *K* family. No differentiation can be shown in group No. 39. In the *Finnish timothy* there are also 4 groups, the height of one of which (No. 45) is slightly different in the I_3 and the *K* family, in the other three

TABLE 32. *Analysis of Variance of the Height of Common Commercial and Finnish Timothy.*

	Number		Height average cm.	Σd^2	D. F.	Variance
	Plants	Families				
Common commercial. Isol. in 1926						
After free flowering. *K*	747	10	106	—	—	—
Within families	—	—	—	42263	737	57,34
Between »	—	—	—	14024	9	1558,22
Total	—	—	—	56287	746	75,45
After isolation I_1	555	10	97	—	—	—
Within families	—	—	—	35915	545	65,90
Between »	—	—	—	30053	9	3339,22
Total	—	—	—	65968	554	119,08
Finnish timothy. Isol. in 1927						
After free flowering. *K*	260	4	107	—	—	—
Within families	—	—	—	24311	256	94,96
Between »	—	—	—	2360	3	786,67
Total	—	—	—	26671	259	102,98
After isolation. I_3	245	4	98	—	—	—
Within families	—	—	—	23744	241	98,52
Between »	—	—	—	24677	3	8225,67
Total	—	—	—	48421	244	198,45

the *I* families show a significantly lower mean than the *K* families. Of *Primus* and *Freja* only one group of each was examined and in both of them the means obtained are significantly lower in the *I* family than in the *K* family. The two groups of *Russian timothy* differ in that one of them (No. 49) shows an intense differentiation while the other (No. 48) exhibits a slight difference without significance.

From the summarizing analysis of variance given in Table 31 it is evident that by grouping the *I* families and the *K* families separately *a greater total variation is obtained in the I material than in the K material.* In the 1926 progenies a significant difference can be shown between the intra-family variances as well as between the inter-family

variances, whereas in the 1927 progenies a significant difference can be shown only between the intra-family variances. The difference found in the intra-family variance in the *I* and *K* material signifies that on the average the variation is greater within the families after isolation than after free flowering. In the 1926 progenies the difference between the interfamily variances shows a more intense differentiation between the families after isolation than after free flowering. In the 1927 progenies it is not possible, however, to show that this differentiation has been greater after isolation than after free flowering.

The analysis of variance of the material combined into groups of one *I* and one *K* family from the same mother plant as given in Table 31 shows that in addition to the differentiation between the *I* and *K* material mentioned above there is also a very great differentiation between the groups. The inter-group variation is much greater than the total intra-group variation. As there exists a great statistical significance it implies that the groups are well differentiated. In spite of the differentiation existing between *I* and *K* families they form together, when derived from the same mother plant, well-defined height populations. This differentiation between the groups is evidently greater than the differentiation between the families within the groups.

In the progenies after the 1926 mother plants the correlation obtained between the mean heights in *I* and *K* from the same mother plant is $r = + 0{,}7748$ (39 pairs) and in progenies after the 1927 mother plants $r = + 0{,}7453$ (49 pairs). Both are very significant. From this it is evident that the mother plants leave their mark very deeply on their progenies not only in isolations but also in free flowering.

The differentiation within each separate strain is more or less pronounced in the various strains. In *Common commercial* (Table 32) the total variation in the *I* material is significantly greater than in the *K* material. The differentiation cannot, however, be shown to be significantly greater between the *I* families than between the *K* families. In the *Finnish timothy* the same conditions prevail as in *Common commercial*, but there also the *I* families are significantly more differentiated than the *K* families. In *Gloria* (Table 33) no such difference can be demonstrated between the *I* and *K* material. In the *Gloria* material from the 1927 mother plants even the total variance is not significantly greater in the *I* material than in the *K* material. In *Kämpe* (Table 34) the differentiation between the families in the *I* and *K* material is approximately the same. Neither in the groups with I_1 families nor with I_3 families can any statistical proof be obtained that

the differentiation is greater in the *I* material than in the *K* material. The total variance in the I_3 material is about the same as that in the I_1 material, as the difference is not significant. In Table 35 it will be finally seen that in strain *121* a difference in the differentiation between the *I* and *K* material can only be demonstrated in the I_2 material from 1926. No such significant difference can be found in the I_3 material.

TABLE 33. *Analysis of Variance of the Height of the Gloria Strain.*

	Number		Height average cm.	Σd^2	D. F.	Variance
	Plants	Families				
Isolations in 1926						
After free flowering. *K*	360	8	97	—	—	—
Within families	—	—	—	22757	352	64,65
Between »	—	—	—	8149	7	1164,14
Total	—	—	—	30906	359	86,09
After isolation. I_1	173	8	82	—	—	—
Within families	—	—	—	14719	165	89,21
Between »	—	—	—	13351	7	1907,23
Total	—	—	—	28070	172	163,20
Isolations in 1927						
After free flowering. *K*	409	4	110	—	—	—
Within families	—	—	—	39039	405	96,39
Between »	—	—	—	14502	3	4834,00
Total	—	—	—	53541	408	131,23
After isolation. I_1	235	4	107	—	—	—
Within families	—	—	—	20336	231	88,03
Between »	—	—	—	3536	3	1178,67
Total	—	—	—	23872	234	102,02

In the latter case the differentiation is greater after free flowering than after isolation, which might however be due to chance variation.

Within each of the strains there is a significant differentiation between the families within the groups as well as between the groups of families derived from the same mother plant.

As already made evident by the various tables the so-called inbreeding effect, *i. e.* the difference in height between *K* and *I* families, seems to vary considerably in the progeny of different mother plants (Tables 29 and 30). Although a statistically demonstrable decrease in height has taken place in the majority of cases after self-fertilization, still in a few cases the height is not significantly different in *I* and *K*

families. After inbreeding of 3 out of 88 mother plants the height is significantly greater in the *I* family than in the *K* family. An exhaustive analysis of variance of the inbreeding effect also shows that the differences in the inbreeding effect in progenies after different mother

TABLE 34. *Analysis of Variance of the Height of Kämpe Timothy.*

	Number		Height average cm.	Σd^2	D. F.	Variance
	Plants	Families				
Isolations in 1926						
After free flowering. *K.*	733	10	113	—	—	—
Within families	—	—	—	59040	723	81,66
Between »	—	—	—	26581	9	2953,44
Total	—	—	—	85621	732	116,97
After isolation. I_1	596	10	106	—	—	—
Within families	—	—	—	65278	586	111,40
Between »	—	—	—	23482	9	2609,11
Total	—	—	—	88760	595	149,18
Isolations in 1927. I						
After free flowering. *K*	280	5	99	—	—	—
Within families	—	—	—	25953	275	94,37
Between »	—	—	—	12760	4	3190,00
Total	—	—	—	38713	279	138,76
After isolation. I_1	218	5	89	—	—	—
Within families	—	—	—	16441	213	77,19
Between »	—	—	—	7211	4	1802,75
Total	—	—	—	23652	217	109,00
Isolations in 1927. II						
After free flowering. *K*	77	2	119	—	—	—
Within families	—	—	—	7679	75	102,39
Between »	—	—	—	308	1	308,00
Total	—	—	—	7987	76	105,09
After isolation. I_2	40	2	113	—	—	—
Within families	—	—	—	3052	38	80,32
Between »	—	—	—	5875	1	5875,00
Total	—	—	—	8927	39	228,90

plants are significant. The results of this analysis are given in Tables 36 and 37. From Table 36 it is evident that the inter-class variance of the inbreeding effect in all strains is considerably greater than the intra-class variance. This is true of the material after the 1926 mother plants and of that after the 1927 mother plants. This difference between

the inter-class and intra-class variance is significant in each individual strain.

In analysing the variation in inbreeding effect between the strains examined it is found (Table 37) that the variation between the strains

TABLE 35. *Analysis of Variance of the Height of the Strain 121.*

	Number		Height average cm.	Σd^2	D. F.	Variance
	Plants	Families				
Isolations in 1926						
After free flowering. *K*	1136	11	102	—	—	—
Within families	—	—	—	88605	1125	78,76
Between »	—	—	—	18275	10	1827,50
Total	—	—	—	106880	1135	94,17
After isolation. I_2	1076	11	91	—	—	—
Within families	—	—	—	108549	1065	101,92
Between »	—	—	—	66875	10	6687,50
Total	—	—	—	175424	1075	163,91
Isolations in 1927. I						
After free flowering. *K*	180	3	105	—	—	—
Within families	—	—	—	18965	177	107,15
Between »	—	—	—	400	2	200,00
Total	—	—	—	19365	179	108,18
After isolation. I_2	123	3	97	—	—	—
Within families	—	—	—	5927	120	49,39
Between »	—	—	—	3952	2	1976,00
Total	—	—	—	9879	122	80,98
Isolations in 1927. II						
After free flowering. *K*	2100	27	109	—	—	—
Within families	—	—	—	267840	2073	129,30
Between »	—	—	—	219555	26	8444,42
Total	—	—	—	487395	2099	232,20
After isolation. I_2	1623	27	99	—	—	—
Within families	—	—	—	228207	1596	142,99
Between »	—	—	—	176560	26	6790,77
Total	—	—	—	404767	1622	249,55

is greater than the total variation within the strains. Although the number of mother plants examined in each strain is small these results may with a certain degree of probability be regarded as indicating that by self-fertilization different strains show on the average a different degree of inbreeding effect.

TABLE 36. *Analysis of Variance of the Inbreeding Effect within Different Timothy Strains in 1929.*

	Intraclass			Interclass		
	Σd^2	D. F.	Variance	Σd^2	D. F.	Variance
After isolations in 1926						
Common commercial strain	78178,00	1282	60,98	9709,23	9	1078,80
Strain 121	197154,00	2190	90,02	14853,26	10	1485,33
Kämpe	124318,00	1309	94,97	11887,20	9	1320,80
Gloria	37476,00	517	72,49	2924,47	7	417,78
After isolations in 1927						
Kämpe	53125,00	601	88,39	5090,71	6	848,45
Strain 121	520939,00	3968	131,29	35308,96	29	1217,55
Gloria	59375,00	638	93,06	6509,34	3	2169,78
Finnish	48055,00	497	96,69	7194,50	3	2398,17
Russian	9837,00	136	72,33	3353,32	1	3353,32

TABLE 37. *Analysis of Variance of the Inbreeding Effect between Different Timothy Strains in 1929.*

	Number of groups	$\Sigma\left(\frac{n_1 n_2}{n_1 + n_2}\right)$	Inbreeding effect average cm.	Σd^2	D. F.	Variance
After isolations in 1926						
Common commercial strain	10	287,4	9,5	87887,23	1291	68,08
Strain 121	11	552,1	11,6	212007,26	2200	96,37
Kämpe	10	312,9	8,0	136205,20	1318	103,34
Gloria	8	105,8	10,6	40400,47	524	77,10
Total within strains	39	1258,2	10,1	476500,16	5333	89,35
Between strains	—	—	—	2752,03	3	917,34
After isolations in 1927						
Kämpe	7	142,9	9,1	58215,71	607	95,91
Strain 121	30	987,8	9,9	556247,96	3997	139,17
Gloria	4	140,2	2,3	65884,34	641	102,78
Finnish	4	125,5	8,9	55249,50	500	110,50
Russian	2	111,5	7,1	13190,32	137	96,28
Total within strains	47	1507,9	8,8	748787,83	5882	127,30
Between strains	—	—	—	7455,01	4	1863,75

Correlation between inbreeding effect and variance in the I family. — In order to ascertain in what degree a decrease in the height of progenies after isolation, as compared with *K* families, is associated

with a wide segregation of various height-types in the progeny the correlations were computed between the inbreeding effect in each group and the variance in the *I* families. The correlations within the separate strains are as follows: —

After isolations in 1926

	Number of pairs	r
Common commercial, I_1	10	$-0{,}1165$
Strain 121, I_2	11	$+0{,}3711$
Kämpe, I_1	10	$+0{,}3951$
Gloria, I_1	8	$+0{,}1938$

After isolations in 1927

Kämpe, I_1 and I_3	7	$+0{,}0548$
Strain 121, I_2 and I_3	30	$+0{,}0943$
Gloria, I_1	4	$-0{,}0924$
Finnish timothy, I_3	4	$+0{,}4568$

The correlations are very unequal but with the small number of pairs examined in each strain no statistical significance can be ascribed to any of the coefficients obtained. As no difference can be shown between the correlations in the different strains in either group of material an average correlation was computed for the 1926 material, which is $r = +0{,}2260$, and another for the 1927 material, this being $r = +0{,}0961$. Since these correlations separately have no statistical significance either and they cannot be shown to be different then the average correlation was calculated, which was found to be $r = +0{,}1550$. This correlation has no significance either, and therefore no significant correlation was found in the material examined.

Calculation of the skewness in height distribution. — The distribution of the height variants after varying degrees of inbreeding was studied in the material tabulated in Tables 38—40. For this purpose the two strains, *Common commercial* and strain *121*, were selected because they contained a relatively large number of individuals. *Common commercial* represents a material not previously inbred and strain *121* comprises progeny families derived partly from I_1 plants and partly from I_2.

From Table 38 it appears that in *Common commercial* an almost normal distribution of the variants is obtained in some cases, in others positive or negative skewness occurs. From the values computed on the skewness it is seen that 6 of the 10 *K* families examined and 3 out

TABLE 38. *Distribution of Height Variants in Swedish Common Commercial Timothy. Progeny of I_0-plants.*

Family No.	Number of individuals in different height classes 65—70—75—80—85—90—95—100—105—110—115—120—125—130—135 cm.															Total	k_1	k_2	k_3	g	m
	14	15	16	17	18	19	20	21	22	23	24	25	26	27							
3739 *K*						2	9	21	31	32	9	5				109	22,18	1,7037	− 0,0943	− 0,0424	± 0,231
40 I_1						4	2	7	4	1	2					20	21,10	2,3158	+ 1,1111	+ 0,2554	± 0,512
41 *K*			1	2	8	15	19	26	17	8	4					100	20,59	2,7898	− 0,7524	− 0,1615	± 0,241
42 I_1	2	7	12	20	38	26	9	1	2							117	17,85	2,2672	− 0,5087	− 0,1490	± 0,224
43 *K*					4	13	21	44	19	15	4					120	21,02	1,8824	+ 0,0256	+ 0,0099	± 0,221
44 I_1			1			4	2	1	3			1				12	20,33	5,1818	+ 2,7272	+ 0,2312	± 0,637
47 *K*				5	7	9	24	28	21	17	8	1				120	21,00	3,1933	− 1,4357	− 0,2516	± 0,221
48 I_1		1	2	6	12	29	24	28	13	5						120	19,88	2,6134	− 1,3246	− 0,3135	± 0,221
49 *K*							1	5	12	13	6		2			39	22,67	1,6053	+ 1,1927	+ 0,5864	± 0,378
50 I_1								1	6	4	17	8	1	1		38	23,84	1,5405	− 0,2568	− 0,1343	± 0,383
51 *K*				1	1	4	10	7	6	5	3	2				39	21,21	3,5263	+ 1,0818	+ 0,1637	± 0,378
52 I_1	1			4	6	5	10	1	6	3	3					39	19,97	5,2895	− 1,0818	− 0,0889	± 0,378
53 *K*						2	7	14	9	7	1					40	21,38	1,4103	+ 0,1350	+ 0,0806	± 0,374
54 I_1			1	8	12	9	8	2								40	18,53	1,5385	− 0,0540	− 0,0283	± 0,374
57 *K*						1	1	17	32	26	26	10	5	2		120	22,97	2,2521	+ 1,1622	+ 0,3439	± 0,221
58 I_1			1	11	13	23	36	22	10	3	1					120	19,74	2,4118	− 0,1453	− 0,0388	± 0,221
59 *K*								2	6	5	3	2	2			20	23,15	2,2632	+ 1,9298	+ 0,5668	± 0,512
60 I_1					1	2	5	3		2	1		1			15	21,00	4,5714	+ 9,8902	+ 1,0116	± 0,580
61 *K*				1			8	7	9	12	3					40	21,75	2,2051	− 2,5641	− 0,7831	± 0,364
62 I_1			1	1	5	4	3	9	7	3	1					34	20,44	3,6970	− 2,8977	− 0,4077	± 0,403

TABLE 39. *Distribution of Height Variants in Strain No. 121 of Timothy. Progeny of I_1-plants.*

Family No.	Number of individuals in different height classes (35–40–45–50–55–60–65–70–75–80–85–90–95–100–105–110–115–120–125–130–135 cm.)																					Total	k_1	k_2	k_3	g	m
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27							
3777 *K*										3	5	7	14	23	26	27	14	1				120	21,59	3,1008	— 2,4954	— 0,4570	± 0,221
78 I_2							1	2	7	15	23	30	19	15	4	2						118	18,85	2,9658	— 0,4347	— 0,0851	± 0,223
82 *K*							1				10	20	28	38	14	5	2	1				119	20,40	2,3136	— 0,9999	— 0,2841	± 0,222
83 I_2				1	1		1	1	5	10	19	24	21	11	4	3	2					103	18,97	4,7941	— 9,6181	— 0,9163	± 0,238
84 *K*										1		6	21	29	28	19	11	2	1			118	21,64	2,3333	+ 0,3999	+ 0,1122	± 0,223
85 I_2									2	7	16	24	28	28	9	5	1					120	19,83	2,5630	— 0,1453	— 0,0354	± 0,221
86 *K*							2	1	2		7	4	15	18	21	24	20	6				120	21,66	5,2017	— 12,8785	— 1,0855	± 0,221
87 I_2						3	3		3	9	14	19	24	17	13	7	2					114	19,54	5,3009	— 8,6382	— 0,7078	± 0,226
96 *K*							3		5	4	12	21	25	32	15	2	1					120	19,81	3,4874	— 5,8453	— 0,8975	± 0,221
97 I_2	2	1		1	3	4	10	15	16	30	18	9	3	3	1	1						117	16,39	6,1026	— 10,4721	— 0,6947	± 0,224
3809 *K*							1		3	2	5	12	23	28	27	12	5	2				120	20,85	3,5378	— 4,4780	— 0,6729	± 0,221
10 I_2					1		1	2	5	8	16	23	32	17	12	2						119	19,36	3,5847	— 5,6457	— 0,8319	± 0,222
11 *K*												1	8	14	24	22	7	2	1			79	22,16	1,9359	+ 0,3025	+ 0,1123	± 0,271
12 I_2									2	4	6	10	15	15	12	6	1	1				72	19,33	3,5493	— 1,2604	— 0,1885	± 0,283
13 *K*										5	5	11	10	17	4	6	2					60	19,25	3,2373	+ 0,1403	+ 0,0241	± 0,309
14 I_2		2	2	4	9	8	7	9	8	1	2		1	1								54	13,87	6,1887	+ 6,8382	+ 0,4442	± 0,324
15 *K*								1	1	3	10	8	21	26	23	15	7	4		1		120	21,05	4,1849	— 1,3673	— 0,1597	± 0,221
16 I_2					1				4	10	9	13	26	26	11	6						106	19,82	3,6952	— 6,1930	— 0,8719	± 0,225
18 *K*										5	13	22	30	32	9	6	2	1				120	20,15	2,4790	+ 1,0597	+ 0,2715	± 0,221
19 I_2					1	6	3	10	20	23	26	19	3	6	1							118	17,20	3,8718	— 1,7215	— 0,2260	± 0,223
22 *K*											3	3	10	9	6	4	4	1				40	21,13	2,3590	+ 1,3225	+ 0,3650	± 0,364
23 I_2						1				2	5	7	10	4	5				1			35	19,71	4,4412	— 1,6815	— 0,1797	± 0,398

of 10 I_1 families show positive values of skewness, but none of them is statistically significant. Of the other families, in which negative values of skewness were obtanied, only one *K* family shows such a high *g* value that it reaches twice its standard error. From the mean values in Table 41 it will be seen that, on the average, no significant values of skewness were obtained in this strain. Nor can any significant difference in the skewness in the *I* and *K* families be shown. Between the values of the skewness in the *I* and *K* families from the same mother plant a rather significant positive correlation (P = 90 : 10) is obtained. The variation of the skewness is insignificantly greater in the *I* material than in the *K* material.

Greater values of skewness were obtained in strain *121* than in *Common commercial*. According to Table 39 negative values are predominant in the progenies after I_1 plants. Among the *K* families only 5 out of 11 show positive figures of skewness without any statistical significance, while the remaining 6 show negative values, 4 of which are statistically significant. One of the I_2 families shows a positive skewness without any significance, the remaining ten showing negative skewness, which is significant in 5 cases. On the average a suggestive negative skewness is obtained in the *K* families and in the I_2 families this skewness is significant. The difference between I_2 and *K* is not significant. A rather significant correlation is found between the values of skewness in *K* and I_2 families from the same mother plant. The variation of the skewness is greater in *I* than in *K*, the difference is however not significant.

In the progeny families after I_2 plants of strain *121* negative values of the skewness were obtained (Table 40) in all I_3 and *K* families, which values are significant in 8 *K* families out of 10 and significant, or at least suggestive, in all the I_3 families. The average values are very significant in the *K* as well as in the I_3 material (Table 41). A significant difference in the k_3 values was obtained between the I_3 and the *K* material, but not in the *g* values. A positive correlation exists between the skewness in the *K* and the I_3 families, although this correlation is not significant with respect to the *g* values. The variation of the skewness is greater in the I_3 than in the *K* material, but the difference is not significant.

From the comparison between *Common commercial* and strain *121* it appears that *Common commercial* does not exhibit any demonstrable skewness in the distribution in I_1 nor in *K*, whereas in strain *121* a rather significant negative skewness is obtained in the progenies after

TABLE 40. *Distribution of Height Variants in Strain No. 121 of Timothy. Progeny of I_2-plants.*

Family No.		Number of individuals in different height classes 35–40–45–50–55–60–65–70–75–80–85–90–95–100–105–110–115–120–125–130–135–140–145–150–155 cm.																									Total	k_1	k_2	k_3	g	m
		8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31							
4831	K								1						2		3	10	5	9	4	3	2	1			40	25,13	6,7179	— 23,8866	— 1,3719	± 0,374
30	I_3								1		1		1	1	1	5	2	2	9	3	2						28	23,32	8,4444	— 30,7122	— 1,2516	± 0,709
33	K								2					2	2	5	14	22	21	19	16	8	3	1	1		116	24,96	5,8174	— 14,7311	— 1,0500	± 0,225
32	I_3		1					1	3	3	5	2	5	10	8	37	24	10	3	1							113	21,30	7,0536	— 31,0677	— 1,6584	± 0,227
35	K							1				1		1	1	5	15	28	27	28	12	15	4	1			139	25,13	4,6522	— 3,3746	— 0,3363	± 0,206
34	I_2							1				1	3	10	17	17	31	11	14	8	3	1					117	22,77	4,6122	— 3,8678	— 0,3905	± 0,224
37	K												1		3	1	5	11	10	7	1	1					40	24,25	3,1282	— 4,1565	— 0,7512	± 0,374
36	I_3									1		3	5	1	3	5	8	4	3								33	21,61	5,6875	— 7,1855	— 0,5298	± 0,408
39	K									1		2	1	3	3	7	15	13	33	23	10	7	2				120	24,60	5,1513	— 11,5966	— 0,9918	± 0,221
38	I_3							1		3	1	5	8	6	10	19	17	21	9	4							104	22,05	6,1068	— 12,7203	— 0,8429	± 0,236
41	K								1					2	13	7	7	15	21	7	5	2					80	23,76	4,8987	— 8,4907	— 0,7831	± 0,269
40	I_3								1	1	2	6	9	4	17	10	13	4	3								70	21,01	4,8261	— 4,5801	— 0,4320	± 0,287
48	K								1	2		2	10	16	24	27	20	12	4	1							119	21,55	3,6186	— 3,9218	— 0,5697	± 0,222
47	I_3								1	1	5	7	7	18	25	22	20	11	1								118	21,13	3,9744	— 4,8515	— 0,6193	± 0,223
50	K			1							1	1	3	5	11	19	32	25	15	4	3						120	22,89	4,6555	— 20,0570	— 1,9967	± 0,221
49	I_3				1			2	2	1	2	3	12	16	20	18	15	14	8	2	1						117	21,34	7,0862	— 16,8308	— 0,8923	± 0,224
69	K					1		1	1	3	4	13	22	17	15	22	10	7	1								117	20,26	5,2155	— 6,3850	— 0,5361	± 0,224
68	I_3			1		1			2	5	4	9	10	13	25	12	6	5	2								95	20,09	6,7234	— 17,3765	— 0,9967	± 0,248
73	K											1	1	13	20	23	20	18	4								100	22,15	2,2525	— 0,4535	— 0,1342	± 0,241
72	I_3			1			1	2	3	2	10	15	9	32	12	12	1										100	19,18	4,9394	— 13,2447	— 1,2065	± 0,241

I_1 plants. After I_2 plants of the same strain a very significant negative skewness is obtained in K as well as in I_3 families. In the material examined here the skewness thus seems to increase with continued inbreeding. Between the g values of the progenies after I_1 plants of strain *121* and those of progenies after I_0 plants in *Common commercial* a difference of $0{,}2942 \pm 0{,}194$ is obtained for K material and $0{,}4241 \pm 0{,}182$ for I material. Between the g values for the progenies after I_2 plants and I_1 plants of strain *121* the differences $0{,}6092 \pm 0{,}224$ (K material) and $0{,}5910 \pm 0{,}184$ (I material) are obtained. The variability of the

TABLE 41. *Mean Values of Skewness in Swedish Common Commercial and Strain No. 121.*

	Swedish common commercial strain	Strain No. *121*	
		Progeny of I_1	Progeny of I_2
K-families, k_3-mean	$+ 0{,}0681 \pm 0{,}433$	$- 2{,}2581 \pm 1{,}261$	$- 9{,}7053 \pm 2{,}444$
» » g »	$+ 0{,}0513 \pm 0{,}129$	$- 0{,}2429 \pm 0{,}145$	$- 0{,}8521 \pm 0{,}171$
I » k_3 »	$+ 0{,}7460 \pm 1{,}119$	$- 3{,}5429 \pm 1{,}547$	$- 14{,}2437 \pm 3{,}185$
» » g »	$+ 0{,}0338 \pm 0{,}127$	$- 0{,}3903 \pm 0{,}131$	$- 0{,}8813 \pm 0{,}129$
Difference of k_3-means (I—K)	$+ 0{,}6779 \pm 0{,}920$	$- 1{,}2848 \pm 1{,}309$	$- 4{,}5384 \pm 2{,}183$
» » g » »	$- 0{,}0175 \pm 0{,}116$	$- 0{,}1474 \pm 0{,}123$	$- 0{,}0292 \pm 0{,}187$
Correlation between k_3 in K- and I-families	$+ 0{,}610$	$+ 0{,}580$	$+ 0{,}729$
Correlation between g in K- and I-families	$+ 0{,}584$	$+ 0{,}563$	$+ 0{,}241$
σ^2 of k_3-mean, K-families	1,8717	17,49	59,74
» » » I »	12,5115	26,34	101,45
σ^2 of the difference of k_3-means (I—K)	8,4675	18,86	47,68
σ^2 of the difference of g-means (I—K)	0,1353	0,1853	0,3508

skewness also increases very markedly in the K as well as in the I families with continued inbreeding.

The differences in skewness between the corresponding I and K families and the differences of their k_1 values (inbreeding effects) are correlated only in the progenies after I_1 plants of strain *121*, where a suggestive negative correlation is obtained between the k_3 differences and the k_1 differences. Between the corresponding g values and the k_1 values a negative correlation is found with a probability of 95 : 5.

Panicle. — In connection with the analyses of fertility an account was given of the length of the panicles in the mother plants in the isolations performed in 1927, when it was shown that the length of

the panicle varies in different plants. The length of the panicle in the progenies was determined on all isolated individuals during the years

TABLE 42. *Analysis of Variance of the Panicle Length in 7 I_2-Families of the Strain 121.*

	Panicle length average mm.	Σd^2	D. F.	Variance
Family No. 3778 Within plants	—	420	10	42,00
Between »	—	822	4	205,50
Total	49	1242	14	88,71
» 3783 Within plants	—	1199	9	133,22
Between »	—	2042	4	510,50
Total	69	3241	13	249,31
» 3785 Within plants	—	734	10	73,40
Between »	—	1140	4	285,00
Total	68	1874	14	133,86
» 3787 Within plants	—	310	10	31,00
Between »	—	4179	4	1044,75
Total	69	4489	14	320,64
» 3810 Within plants	—	452	10	45,20
Between »	—	4368	4	1092,00
Total	54	4820	14	344,29
» 3814 Within plants	—	685	10	68,50
Between »	—	1188	4	297,00
Total	60	1873	14	133,79
» 3819 Within plants	—	590	10	59,00
Between »	—	888	4	222,00
Total	72	1478	14	105,57
All the families				
Within plants within families	—	4390	69	63,62
Between » » »	—	14627	28	522,39
Total within families	—	19017	97	196,05
Between families	—	6924	6	1154,00
Total	63	25941	103	251,85

1929 and 1930, in addition to which some families were analysed in their entirety with respect to this character. Table 42 contains a summarizing analysis of variance of the length of the panicles in 7 I_2 families of strain *121*. Both the single plants and the families are

characterized by special averages, which as far as the families are concerned are statistically significant. The inter-plant variance in all the families is greater than the intra-plant variance, and the average difference between them is significant. A hereditary differentiation can be assumed to have taken place between the plants with a segregation of types having a varying propensity for the length of the panicle. It appears, however, as if this differentiation varies in degree in different families, as the inter-plant variance differs very greatly between the individual families.

For computing the correlation between the panicle length in the mother plants in 1927 and the progenies in 1929 there were only 7 pairs available, and in these the correlation is $r = + 0{,}6665$. With such a small number of pairs no great statistical significance, it is true, can be ascribed to this correlation (probability 89 : 11), but as the measure-

TABLE 43. *Analysis of Variance of the Panicle Length in Isolated Timothy Plants in the Year 1930.*

	Σd^2	D. F.	Variance
Within plants within families	44325,00	182	243,54
Between » » »	12005,00	23	521,96
Total within families	56330,00	205	274,78
Between families.....	62812,00	14	4486,57
Total	119142,00	219	544,03

ments were made in different years and nevertheless such a decidedly positive correlation is obtained the correlation seems to be strongly suggestive.

Table 43 presents a summarizing analysis of variance in the length of the panicles in plants isolated in 1930, and from this table it is seen that even in the material examined here a great differentiation occurs between the plants within the families as well as between the families themselves. Even if the variation within the families is great they nevertheless constitute populations with significantly different averages.

Correlations. — As already mentioned above a positive correlation occurs between the seed setting after isolation and after free flowering in the 1927 material. As the differentiation in height and in the length of the panicles is also very pronounced it is of great interest to investigate whether the variation in one character depends on the variation in another character.

In conjunction with the analysis of fertility carried out on the 1927 material the correlation was examined between »self-fertility» and length of panicle, and in the material examined these characters were shown to be independent of each other (cp. p. 49).

In the material examined in 1929 in respect of fertility correlations were computed between height and length of panicle and between height and seed setting in free inflorescences. Owing to the fact that only a few plants in each family were examined in all characters there is no possibility of showing correlations in all families, because such a small number of pairs cannot ensure any statistical significance for any possibly occurring weak correlations. In families in which at least 5 plants were examined the correlation coefficients were however calculated, and these are as follows: —

Correlations: 1929.

Family No.	Number of pairs	Height and panicle length	Height and general fertility
3778	5	+ 0,7030	+ 0,3965
3783	5	+ 0,6058	+ 0,6057
3785	5	+ 0,3650	+ 0,6452
3787	5	+ 0,6088	+ 0,5235
3810	5	+ 0,4176	+ 0,2766
3814	5	— 0,1678	+ 0,5689
3819	5	+ 0,7978	+ 0,6409
4874	7	+ 0,7694	+ 0,7398
4880	5	+ 0,6685	+ 0,6355
4884	5	+ 0,6721	+ 0,6935
4985	5	+ 0,0350	+ 0,3732
4990	5	+ 0,4534	+ 0,4855

The correlations between height and length of panicle are, with but one exception, positive and in all the families the correlations between height and seed setting in free inflorescences are also positive. The values, however, are not statistically significant owing to the small number of pairs. However, as no significant differences can be obtained between the correlations in the different families a total correlation coefficient was computed for all of them. The values thus found are $r = + 0{,}5577$ for height and length of panicle and $r = + 0{,}5703$ for height and fertility. These correlation coefficients have great significance ($P > 99 : 1$), for which reason it can be considered as

proved that in the material tested the three characters mentioned above do not vary independently. Hence, the conclusion can be drawn that both the variation in panicle length and the variation in seed setting are associated with the variation in height.

The variation in families more closely examined. — The progenies of two I_2 plants of strain *121* isolated in 1927 showed themselves to be exceedingly variable in several characters, and therefore each plant of the I_3 families and of the corresponding *K* families was closely examined with respect to the length of their panicles and the tillering in addition to the height. The I_1 family No. 4933 mentioned above from *Kämpe* was also closely analysed. Unfortunately, this family has no corresponding *K* family but by way of comparison the measurements of the mother plant are given instead.

Group I, comprising families 4876 and 4877. — According to Table 30 the I_3 family 4876 is on the average lower than the corresponding *K* family 4877, and the difference between their mean heights is significant. The I_3 family, however, is also less vigorous in other respects. For instance, of this family 27,2 % of the individuals planted out had died out after the winter of 1928—29, while of the *K* family only 3,3 % had died. Of the remaining 40 plants in the I_3 family only 16 of them were entirely green, the others being more or less chlorophyll-deficient, the panicles being wholly or partly albino. Among the 58 plants in the *K* family there were 4 plants with more or less albino panicles. The mother plant, isolated in 1927, had been recorded as having albino panicles and it was evidently heterozygous with respect to the capacity of chlorophyll development in the panicles. Judging from the numerical proportion, 16 green : 24 albino, it seems as if a monohybrid segregation had occurred. If this is the case then we can assume that the 24 individuals are heterozygotes and that the homozygously albinotic individuals were less vital and had been eliminated. That the *K* family does not show more than a few plants with albino panicles may be due to extensive crossing between the mother plant and male individuals with some other factor, which causes the normal development of the chlorophyll even in the heterozygous stage for the assumed factor for albino panicles.

Besides the variation in development of chlorophyll there occurs also a pronounced variation in other characters. Three plants in the I_3 family were recorded with very weak tillering, and the variation in height, panicle length and tussock formation is very great.

The analysis of the length of the panicle is summarized in Table 44,

from which it is seen that the intra-plant variation in the I_3 as well as in the *K* family is small in proportion to the great interplant variation. The differences have very great statistical significance. The calculated intra-plant variation does not comprise the whole of the variation

TABLE 44. *Analysis of Variance of the Panicle Length of two I_3-Families and Corresponding K-Families of Strain 121.*

	Number of plants	Panicle length average mm.	Σd^2	D. F.	Variance
Family No. 4876 I_3	40	58			
Within plants	—	—	2436	80	30,45
Between »	—	—	29952	39	768,00
Total	—	—	32388	119	272,17
Family No. 4877 K	58	75	—	—	—
Within plants	—	—	7134	116	61,50
Between »	—	—	30423	57	533,74
Total	—	—	37557	173	217,09
Group I 4876—4877	98	68	—	—	—
Total within families	—	—	69945	292	239,54
Between families ...	—	—	20526	1	20526,00
Total	—	—	90471	293	308,77
Family No. 4882 I_3	86	71	—	—	—
Within plants	—	—	3531	169	20,89
Between »	—	—	74241	85	873,42
Total	—	—	77772	254	306,19
Family No. 4883 K	149	76	—	—	—
Within plants	—	—	4035	295	13,68
Between plants	—	—	154520	148	1044,05
Total	—	—	158555	443	357,91
Group II 4882—4883	235	74	—	—	—
Total within families	—	—	236327	697	339,06
Between families ...	—	—	4071	1	4071,00
Total	—	—	240398	698	344,41

occurring within the plants, because only 3 of the panicles were examined. However, as the corresponding panicles on the 3 tallest stems of all plants were examined the limited variability within the plants can no doubt be employed for the purposes of comparison with the variation between those plants measured in the same manner. The existence of a greater inter-plant variation in the I_3 family than in the

K family may be regarded as indicating a more intense differentiation between the plants after isolation, but the difference is not great enough to have any significance. The two families exhibit quite different averages for the length of the panicle, 58 and 75 mm. respectively.

The tillering capacity of the families, which was determined by measuring the circumference of the plants after pressing the straws together, varies considerably in both families. The average of the inbred family is 23 cm. with a variance of 90,82, and that of the *K* family 34 cm. with a variance of 89,14. The variability is therefore equally large in both families but the average is considerably lower in the I_3 family than in the *K* family. The united inter-plant variation within the families in the group amounts to $\sigma^2 = 89{,}82$ (D. F. = 96), while the inter-family variation is $\sigma^2 = 2890{,}00$ (D. F. = 1). The difference between these variances is significant and so it can be inferred that the averages of the families are unequal and that therefore the tillering is considerably poorer in the I_3 than in the *K* family.

Thus, the families in this group differ, among other things, in the I_3 family being lower and having shorter panicles and poorer tillering than the *K* family.

Group II, comprising families 4882 and 4883. — These two families, the former an I_3 family and the latter a *K* family, are derived from the second I_2 plant of strain *121* mentioned above. In this group the effect of inbreeding has manifested itself in a similar manner to that in Group I. In contradistinction to Group I, however, Group II exhibits no chlorophyll variation, all individuals being apparently normal in this respect. Other sub-lethal individuals appear, however, which can be seen, inter alia, in their impaired winter hardiness. Out of 159 individuals of the I_3 family 4882 planted out 73 died during the winter of 1928—1929, which is equal to a mortality of 45,9 %. The mortality of the *K* family 4883 for the same period is only 6,9 %. From this it is evident that the vegetative vigour of the inbred family is lower and this is also evident in the other analysed characters. The average height is lower in the I_3 family, Table 30, and the difference is significant. Table 30 also shows that the variation in height is greater in the *K* family, and although the difference is not significant it is at any rate suggestive.

From the analysis of the length of the panicle in Table 44 it is seen that the total mean of the I_3 family 4882 is 71 mm. and that of the *K* family 4883 is 76 mm. Both the total variation and the inter-plant variation are greater in the *K*-family, but no statistical significance can

be found for the differences. The inter-plant variation in both families is, however, significantly greater than the intra-plant variation. At the bottom of Table 44 is seen how great a difference exists between the inter-family and the intra-family variation and this difference is very significant, for which reason the two families can be considered to have different average lengths of panicles.

In the I_3 family the average of the circumference of the tussock is 22 cm. and in the *K* family 28 cm. with a variance of 131,53 (D. F. = 85) and 254,43 (D. F. = 148) respectively. The differences between the averages and between the variances are significant. Thus, it can be shown that in this character the *K* family has a higher mean value and is more variable than the I_3 family.

The analyses of Group II have thus supplied evidence that an inbreeding effect occurs, which could be measured in winter hardiness,

TABLE 45. *Correlation Coefficients in the Families 4876, 4877, 4882 and 4883.*

	Group I		Group II	
Family No.	4876 I_3	4877 *K*	4882 I_3	4883 *K*
Number of pairs	40	58	86	149
Height and panicle length	+ 0,7021	+ 0,6629	+ 0,7638	+ 0,7523
Height and tillering	+ 0,6229	+ 0,5912	+ 0,7182	+ 0,3538
Panicle length and tillering	+ 0,2709	+ 0,3766	+ 0,5942	+ 0,6615

height, length of panicle and tillering. The mean values of these characters are in general lower in the I_3 family and indicate a lower degree of vigour than in the *K* family, but the latter exhibits the greater variation.

Correlations in Group I and II. — In order to investigate whether the inbreeding effect is manifested simultaneously in several characters the coefficients of correlation were calculated between height and length of panicle and between height and tillering. The correlations found are given in Table 45. All the correlations are found to be positive and have great statistical significance. Thus, the probability that correlations really exist is more than 99 : 1, except in one instance, viz. between the panicle length and tillering in family 4876, in which the probability in 40 pairs is only about 90 : 10. The most pronounced correlation is between the height and the length of the panicle, and this correlation is of the same magnitude in the families tested. A very

great part of the variation in the length of the panicle is therefore dependent of the variation in the height. The analysis of inter-plant variation in the length of the panicle in family 4876 is presented here: —

	Σd^2	D. F.	Variance
Total interplant	29952,00	39	768,00
Regression upon height	15537,60	1	15537,60
Remaining interplant	14414,40	38	379,33
Intraplant	2436,00	80	30,45

The remaining interplant variance is significantly greater than the intraplant variance, which shows that, independent of the height, a marked variation in panicle length occurs between the plants.

The correlations between height and tillering are of the same magnitude in both families of Group I, but in Group II there is a great difference between the correlation coefficients of the I_3 and K families. z of this difference is 0,5331 with a standard error of $\pm$ 0,1375, hence there exists a great significance for the difference between these correlations. In the I_3 family the height of the plant and the tillering are therefore more closely correlated than in the K family.

The direct correlations between the length of the panicle and the tillering are the same in both the I_3 and the K family in each group, but between the groups there is a divergency with a weaker correlation in Group I than in Group II. This difference is certainly not of an incidental nature, as z of the difference between the two I_3 families amounts to 0,4063 $\pm$ 0,1997 and between the K families to 0,3995 $\pm$ 0,1582. Thus we have here a case in which the correlations can be considered to be of different strength in progenies after two different mother plants.

The partial correlations between panicle length and tillering, after eliminating height, are for family 4876 — 0,2398, for 4877 — 0,0253, for 4882 + 0,1015 and for 4883 + 0,6415. Only in families 4876 and 4883 is it possible to attach any statistical significance to these correlations, but of these it appears that in one case the length of the panicle and the tillering are correlated negatively and in the other case positively.

The I_1 family 4933 from Kämpe. — Of all inbred families examined the I_1 family 4933 exhibits the most extensive and most conspicuous variation with a plainly perceivable effect of inbreeding in a number of characters. It was therefore analysed very closely first in 1929 and then in 1930. Unfortunately, there is no K family

for the purpose of comparison but the mother plant 4680 was vegetatively propagated and used for comparison in the various characters. The characters subjected to a close examination are, fertility, height of plant, tillering and length of the panicle.

The degree of fertility was investigated in 20 plants after free flowering in 1929 and was then found to be very low, on the average only 4,5 seed per panicle cm. being harvested. In the same year measurements were obtained of the other characters, and after all plants had been clonally propagated in the autumn of 1929 six plantlets were obtained of each clone. In 1930 the »self-fertility» of all clones was studied, the results of which have been mentioned on page 59. Re-measurements of the height were carried out in 1930, while also a measurement of the length of the panicles was obtained in the same year during the fertility tests.

Of the 80 plants planted out in 1928 75 were still alive in 1929. Several of them were, however, delicate and in the following winter 7 more died off (dwarf-plants) so that in 1930 only 68 individuals remained. The vigour of the plants was very variable, manifesting itself in a pronounced variation, for instance, in the height and tillering of the plants and in the development of their panicles. No variation in chlorophyll occurred, however, all individuals appearing to be normally green. Some abnormalities appeared in respect to the development of the panicles. Of the 68 individuals examined in 1930 four developed only small dwarfy panicles with abnormal florets, which dropped at flowering time, leaving the rachis entirely bare. These plants represent one extreme with regard to fertility, transitional types of all kinds being found right up to almost full fertility.

The average height in 1929 amounted to 91 cm. with a variance of 346,09. Hence, the variation in height is very great, which is also evident from the analysis made in 1930, when an average of 78 cm. was obtained, with a variance of 358,71. A comparison between the two years will show that the variation is approximately equal. In 1929 the minimum and maximum heights were 31 and 121 cm. and those of 1930 were 26 and 108 cm. In 1930 when 2 plantlets of each individual were measured a measurement was obtained of the variation between the plantlets and that between the clones. The total variance between the plantlets within the clones was 41,21 (D. F. = 68) while that between the clones was 716,77 (D. F. = 67). The difference between them is significant.

In 1930 the mother clone 4680 showed an average height of 96 cm.

with a variance of 13,00 between the plantlets. The interclass variance obtained between the mother clone and its progeny clones is then 714,00 (D. F. = 1), while the intraclass variance will be only 356,17 (D. F. = 136). This difference is, however, not statistically significant and therefore it cannot be proved for certain that the family 4933 has a lower average height than the mother plant.

The total mean of the length of the panicles in 1929 amounts to 57 mm. with $\sigma^2 = 253{,}17$. The main part of this total variance belongs to the interplant variation, which has a variance of 745,05 (D. F. = 74), and only a small part to the intraplant variation. In 1930 the total mean of the length of the panicle was 88 mm. The analysis of variance is found in Table 46, from which it will be seen that the greatest part of the variation is inter-clone variation. As the difference between

TABLE 46. *Summarizing Analysis of Variance of Panicle Length in the Timothy Family No. 4933.*

	Σd^2	D. F.	Variance
Within plantlets within clones	19508,00	248	78,66
Between » » »	7548,00	64	117,94
Total within clones	27056,00	312	86,72
Between clones	140734,00	63	2233,87
Total	167790,00	375	447,44

this variation and the total intra-clone variation is significant, the difference between the inter-clone variation and the inter-plantlet variation likewise statistically significant, it is therefore evident that the differentiation in the panicle length between the clones is considerable. Within the clones the variation in the length of the panicle is greater between the plantlets than within them, the difference even here being significant. Still, this increase is small in proportion to the wide difference existing between the inter-clone and the intra-clone variations, and therefore a differentiation between the clones seems to exist even if it turned out that the environment increases the variation between the clones to a somewhat greater extent than between the plantlets.

In 1930 the average length of the panicles of the mother clone 4680 was 98 mm. with $\sigma^2 = 49{,}00$. An interclass variance of 600,00 (D. F. = 1) is obtained between the mother clone and its progeny clones, while the total intraclass variance will be 442,20 (D. F. = 380). The difference between these variances has no statistical significance

and it cannot therefore be maintained that the progenies have shorter panicles than the mother plant.

The tillering was examined only in 1929 by measuring the circumference of all the plants. The average circumference obtained was 29 cm. with $\sigma^2 = 78{,}41$. Thus, the variation is very great, with a range from 4 cm. to 46 cm.

Correlations. — Correlations were determined, first, between the same characters in different years and second, between different characters in the same year, the coefficients of correlation thus obtained are given in Table 47. All the correlations computed are positive and in the majority of cases the statistical significance is great enough to prove that correlations really exist. The height of the plants and the

TABLE 47. *Correlations in the I_1 Family No. 4933.*

	Number of pairs	r	Probability of the correlation
Height in 1929 and height in 1930	68	$+0{,}6907$	99 : 1
Panicle length in 1929 and in 1930	64	$+0{,}6565$	99 : 1
Height in 1929 and general fertility in 1929	20	$+0{,}4242$	90 : 10
Height in 1929 and panicle length in 1929	64	$+0{,}4877$	99 : 1
Height in 1929 and tillering in 1929	64	$+0{,}4010$	99 : 1
Height in 1930 and »self-fertility» in 1930	64	$+0{,}4044$	99 : 1
Height in 1930 and panicle length in 1930	64	$+0{,}6097$	99 : 1
Panicle length in 1929 and tillering in 1929	64	$+0{,}2789$	95 : 5
Panicle length in 1930 and »self-fertility» in 1930.....	64	$+0{,}3269$	99 : 1

length of the panicles were examined in both years and the correlations between the plants in both years are equally great for both characters. Assuming that the correlations obtained are those really occurring the total variation in each character can be divided into hereditary variation and remaining variation, which can be considered to have arisen from casualities and environmental conditions. As regards the variation in height it will be found that in such a division of the total variation, after deducting the common variation, the remaining interplant variation in 1929 will be $\sigma^2 = 263{,}96$ and in 1930 $\sigma^2 = 369{,}95$. This variation is somewhat greater in 1930 but no statistically significant difference can be shown, and therefore this variation may be regarded as approximately the same in both years. As already mentioned above (p. 88) the variation between the plantlets within the clones was in 1930 found to be $\sigma^2 = 41{,}21$. By comparing this variation and the

variation not correlated between the years in 1930, $\sigma^2 = 369{,}95$, it will be found that the latter is significantly greater than the variation between the plantlets.

In dividing the variation in the length of the panicle in 1929 and 1930 we encounter the same state of affairs as in the variation in height. In 1929 the non-correlated variation between the plants is greater than the intraplant variation with a statistically significant difference and in 1930 the corresponding variation is greater between the clones than between the plantlets within the clones. In the latter case the variances are 1182,29 and 117,94 respectively with 62 and 64 D. F. The difference is significant and these variances can therefore be regarded as unequal.

Between the height of the plant and the seed setting on open pollination in 1929 there is a correlation of $+ 0{,}4242$, which shows that the fertility is not independent but that it is associated with the height of the plant. The great variation in seed setting not correlated with the variation in height indicates, however, that an independent hereditary variation may also occur. The remaining interclass variation amounts to $\sigma^2 = 538{,}69$ and it does not seem probable that this is entirely caused by environmental conditions, inasmuch as the plants have the same facilities of fertilization and only slight differences in earliness can be observed within the family. The total intraplant variance is only 11,84 (D. F. = 40).

In both 1929 and 1930 the correlations between height and length of panicle are about equally great, $+ 0{,}49$ and $+ 0{,}61$ respectively. Nor can any statistical significance be ascribed to the difference found between them. The interplant variation in the length of the panicle correlated with the height in the 1929 material amounts to $\sigma^2 = 8333{,}61$ and the remaining interplant variation is $\sigma^2 = 413{,}18$ (D. F. = 62). From the correlation between the length of the panicle in 1929 and 1930 a maximum value of the environmental variation, in 1929, of $\sigma^2 = 304{,}12$ (D. F. = 62), is calculated. Thus, the interplant variation, which is independent of the variation in height, obtained now is greater than the variation caused by chance and environment between the plants. The surplus variation may then be assumed to be due to free hereditary variation. This cannot, however, be positively shown to be the case, as the difference is not significant. It is therefore not possible to show that free hereditary variation in the length of the panicle occurs. In 1930 the variation in the length of the panicle not correlated with the height is $\sigma^2 = 1344{,}80$ (D. F. = 62) between

the clones and the calculated maximum value of the environmental variation between the clones is $1182{,}_{29}$ (D. F. $= 62$). The difference is not significant and neither in 1930 can any independent hereditary variation in the height of the panicle be shown to occur.

The correlation between height and tillering in 1929 is somewhat less than between height and length of panicle, still no statistically significant difference can be obtained. The greater portion of the variation in tillering, $\sigma^2 = 823{,}_{68}$, is connected with the variation in height and the remaining variation, $\sigma^2 = 66{,}_{73}$, is most probably mainly or wholly modificatorily enforced.

The direct correlation between the length of the panicle and the tillering is $+ 0{,}_{2789}$. If the height is eliminated the partial correlation (FISHER 1930) is only $+ 0{,}_{1042}$ and between these characters no correlation can therefore be shown over and above their common connection with the height.

The correlations between height and »self-fertility» and between length of panicle and »self-fertility» are of about the same magnitude and their difference is not significant. From the former correlation it can be computed that the inter-clone variation in »self-fertility» correlated with the variation in height is $\sigma^2 = 4097{,}_{88}$ and the remaining inter-clone variation $\sigma^2 = 318{,}_{30}$ (D. F. $= 62$). According to Table 28 the variation found between the plantlets is only $\sigma^2 = 15{,}_{96}$ (D. F. $= 64$). The difference between the remaining inter-clone variation and the interplantlet variation is significant and it is therefore probable that a free hereditary variation in »self-fertility» also occurs.

The direct correlation between the length of panicle and self-fertility is $+ 0{,}_{3269}$, the partial correlation, if the height is eliminated, is $+ 0{,}_{1108}$ and between these characters no correlation can therefore be shown over and above their joint connection with the height.

The correlations calculated show that the characters examined vary in a very high degree along parallel lines.

Progenies after mother plants selected in 1928.

Practically no seed was obtained from the isolations performed in 1928 and therefore no new inbred material could be raised. From the seed produced in free flowering by the selected mother plants some *K* families were procured and these were planted out so as to obtain material for comparison with the clonally propagated mother plants. In 1930 measurements were carried out on this material and simultaneously on populations of spaced plants of the original *Kämpe*

population and its derivative strain *404*. The results of these measurements are presented in tabular form in Table 48, in which are given the mean heights of the mother clones and of the families examined, along with the variation within each family and group of mother plants and progeny. As seen in this table the *K* families raised are on the whole taller than the I_3 and the I_2 mother clones. The variation is also very great in the majority of the *K* families. In dividing the total variation within each group, formed by a mother clone and its progeny family, it is found that the interclass variance, with one exception, is greater than the intraclass variance. In 4 of the

TABLE 48. *Analysis of Variance of the Height of Timothy Material in the Year 1930.*

Group No.	Field No.	Basic population	Inbreeding generation	Number of plants	Average height cm.	Variance	Group average cm.	$Var._t$	$Var._{ab}$	$Var._p$
1	5510	Kämpe	I_3M	2	42	25,00	99	274,62	174,88	6758,00
	537	»	*K*	65	101	177,22				
2	5512	»	I_3M	2	48	8,00	96	84,06	106,43	5980,00
	538	»	*K*	7	110	122,83				
3	5513	»	I_3M	2	66	98,00	104	240,04	200,10	2956,00
	539	»	*K*	68	105	201,63				
4	5515	»	I_3M	2	42	5,00	94	361,75	208,57	5723,00
	540	»	*K*	35	97	214,56				
5	5516	»	I_3M	2	60	145,00	79	375,10	282,00	938,00
	541	»	*K*	6	85	309,40				
6	5517	Strain 121 ...	I_2M	2	79	8,00	90	325,48	326,51	242,00
	543	» » ...	*K*	81	90	330,49				
7	560	Kämpe	I_0	136	96	172,27	92	199,33	179,89	5001,00
	561	Strain 404 ...	I_2	113	87	189,07				

groups there is a great statistical significance for the difference, in the fifth the difference has no statistical significance with the low number of D. F. and in the sixth group, from strain *121*, the intraclass variance is somewhat greater than the interclass variance. In the last two cases no differences in height can therefore be shown, but in the other groups the height of the mother plants can undoubtedly be considered to be different from that of the *K* families. This indicates that the *K* families show a luxuriance in height as compared with the previously inbred mother plants.

The difference in height between *Kämpe* and strain *404* is great enough to give rise to an interclass variance that is significantly greater than the total intraclass variance. These strains can be regarded as

belonging to different height populations. Strain *404*, inbred for two generations, is on the average lower than the mother population, which does not imply, however, that strain *404* is less vigorous and less productive. On the contrary, the yield tests carried out have shown that strain *404* produces on the average about 10 % more green matter than *Kämpe* (ÅKERBERG 1933, where *404* is called *Kämpe II*).

Progenies after mother plants selected in 1929.

As appeared from the account given of »self-fertility» the seed setting in isolations on the mother plants selected in 1929 was in several cases very low, the result of which is that only small families of *I* plants are available, and in quite a large number of cases it has only been possible to grow progenies after free flowering. The investigations concerning the effect of inbreeding embrace germination tests and examinations of the height of the developed plants in 1931, comparisons being also made between mother clones and their derivative *I* and *K* progenies.

Germination capacity and defective seedlings. — The germination of seeds after isolation and after free flowering was studied in such a manner that the seeds, instead of being sown in sterilized earth, were germinated in a Jacobsen's incubator and the seedlings were planted in pots. Records were made of the number of seedlings and the chlorophyll development was also noted. In order not to have too great a material after free flowering the number of seeds was limited to 60, this being considered sufficient provided the germination was high and that the majority of the developed seedlings could be kept alive. The germination proved to be very variable in seeds after isolation and after free flowering. Seedlings were raised from 39 mother plants after isolation and after free flowering and the germination is quite comparable inasmuch as the seeds were harvested simultaneously and kept under exactly the same conditions. After these 39 plants the germination after isolation was on the average somewhat higher than after free flowering. The average after isolation was 80,4 % with a variance of 526,58 and after free flowering 74,7 % with a variance of 399,89. The difference is, however, too small for any statistical significance to be ascribed to it. The greater variability in the material after isolation has no statistical significance either. The correlation between the germination of the material after isolation and that of the material after free flowering is $r = + 0{,}5658$. In 39 pairs the probability for the existence of this correlation is more than 99 : 1.

Plants having a low degree of germination in isolated seed thus also show a low degree of germination in non-isolated seed.

The occurrence of chlorophyll variants was recorded in altogether 26 families, 13 of which had been grown from seed after isolation, 12 from seed after free flowering of I_2 and I_3 mother plants, and 1 consisted of the *Kämpe* population. The number of chlorophyll

TABLE 49. *Number of Chlorophyll Variants in Timothy Families Sown in the Year 1930.*

Family No.	Strain	Inbreeding generation	Number of seedlings			
			Green	Yellowish green	White	Total
1206	121	I_2K	54	—	1	55
1219	»	I_3	33	3	1	37
1226	»	I_3	45	1	6	52
1228	»	I_3	12	—	1	13
1230	»	I_3	49	1	1	51
1243	»	I_3	22	1	2	25
1246	»	I_2K	40	—	1	41
1252	»	I_3	53	1	—	54
1254	»	I_2K	25	—	1	26
1262	»	I_2K	57	—	1	58
1287	»	I_4	10	—	4	14
1294	»	I_4	24	—	11	35
1296	»	I_3K	16	—	3	19
1297	»	I_3K	13	—	3	16
1298	»	I_3K	19	—	1	20
1299	»	I_4	58	—	1	59
1303	»	I_3K	49	—	1	50
1307	»	I_4	6	—	1	7
1311	»	I_4	39	—	6	45
1312	»	I_3K	38	—	3	41
1314	»	I_3K	53	—	1	54
1318	»	I_3K	24	—	2	26
1345	»	I_4	42	—	5	47
1338	Finnish...	I_3K	38	—	1	39
1341	» ...	I_4	59	—	1	60
1359	Kämpe ...	I_0	48	—	1	49

variants in these families will be found in Table 49, where I_2K and I_3K denote families derived from I_2 and I_3 mother plants respectively after free flowering. The segregation of chlorophyll-deficient individuals seems to be due to heterozygosity in one or more factors in the mother plants. In certain families it seems possible to assume that a monofactorial segregation has occurred, while it is difficult to form any definite opinion with regard to the other families. It seems beyond doubt that a segregation in at least two factors has occurred in a number

of families, and this is corroborated by the appearance of single light-green individuals in 5 of the families.

When transplanting the seedlings in the open in the summer of 1930 the mother plants were vegetatively propagated and from each of these plants 10 cuttings of about the same size as the seedlings were planted so that the mother clones and progenies were afforded exactly the same conditions to develop their tussocks for the following year.

In 1931 measurements were obtained of the height of all mother clones and progeny families in the material. The material has been divided according to the different generations of inbreeding and according to the basic population employed. The greater part of the material is derived from strain *121*, which, as already mentioned, exhibited the highest degree of self-fertility and also contained several practically valuable characters, which was the reason why this strain was especially subjected to selection in 1929.

Height.

Strain 121. — Table 50 contains the results of the measurements of I_2 mother clones and their derivative K and I_3 families of strain *121*, in addition to which an analysis of variance is given of the individual clones and families and of groups of clones and families brought together in different ways. Thus, groups have been formed of I_2 mother clones and K families, I_2 mother clones and I_3 families and K families and I_3 families in order to obtain a comparison between the height of the clones and of the respective families. The designations for interclass variances and intraclass variances employed in Tables 50, 51 and 57 are the following, var_{MK}, var_{MI} and var_{KI} correspond to the intraclass variance of groups of mother clone and K family, mother clone and I family and K and I families respectively. $var_{M/K}$, $var_{M/I}$ and $var_{K/I}$ denote the corresponding interclass variances in the groups. I_2M and I_3M are I_2 and I_3 mother clones respectively.

The differences in the average heights are, owing to the small number of plants, rather difficult to determine for certain, but in the majority of cases it is possible to obtain statistically significant values. Between I_2 mother clones and K families 23 comparisons have been made, 17 of which show a higher average in the K families, in one case the height is the same in the mother clone and the K family, while in 5 the height is lower in the K families than in the mother clones. In 12 of the first-mentioned 17 cases the difference in height is significant. The differences in the other 5 groups have no statistical significance and may have arisen entirely from casualities and modifications. Of the 5 groups in which the K families are lower the difference is significant only in 1. In 13 groups we can

TABLE 50. *Analysis of Variance of the Height of I_2-Mother Clones, I_3- and K-Families in Strain No. 121. Measurements in 1931.*

Group No.	Field No.	Inbreeding generation	Number of plants	Average height cm.	Variance	Average MK	var_{MK}	$var_{M/K}$	Average MI_3	var_{MI_3}	$var_{M.I_3}$	Average KI_3	var_{KI_3}	var_{K/I_3}
1	5518	I_2M	10	102	32,00	97	106,43	289,00	91	29,86	3376,00	93	112,65	2997,00
	1208	K	39	96	124,05									
	1207	I_3	6	72	26,00									
2	6034	I_2M	8	58	37,57	70	90,16	1789,00	59	38,67	35,00	74	109,64	540,00
	1216	K	13	77	120,83									
	1215	I_3	3	62	42,50									
3	6035	I_2M	9	57	243,75	77	164,93	5008,00	58	217,56	107,00	83	129,14	736,00
	1218	K	22	85	134,90									
	1217	I_3	2	65	8,00									
4	6041	I_2M	10	98	28,67	93	67,55	342,00	93	67,58	426,00	90	89,37	34,00
	1227	K	23	91	83,41									
	1226	I_3	11	89	102,50									
5	6042	I_2M	9	75	235,00	85	154,34	1225,00	75	230,50	12,00	87	131,35	676,00
	1229	K	22	89	123,62									
	1228	I_3	3	73	212,50									
6	6043	I_2M	9	94	270,00	91	129,88	99,00	80	159,36	2724,00	82	65,58	2652,00
	1231	K	18	90	52,18									
	1230	I_3	15	72	81,86									
7	6044	I_2M	10	99	98,11	92	146,58	511,00	94	122,00	655,00	91	169,63	264,00
	1233	K	21	93	168,40									
	1232	I_3	5	85	175,75									
8	6045	I_2M	10	80	61,78	94	107,85	2472,00	81	108,87	32,00	91	124,38	3350,00
	1235	K	32	98	121,23									
	1234	I_3	22	82	129,05									
9	6047	I_2M	10	87	34,44	90	71,00	414,00	84	32,27	522,00	87	117,40	1251,00
	1238	K	4	99	180,67									
	1237	I_3	3	72	22,50									
10	6050	I_2M	9	88	105,12	88	256,00	0	88	105,12	0	—	—	—
	1242	K	13	88	356,92									
	1241	I_3	1	88	—									
11	6063	I_2M	9	72	62,87	86	141,85	2276,00	65	165,89	873,00	82	182,81	8396,00
	1262	K	32	90	162,23									
	1261	I_3	12	59	240,82									
12	6065	I_2M	10	70	78,22	74	131,16	336,00	69	88,50	28,00	76	179,00	244,00
	1266	K	11	78	178,80									
	1265	I_3	2	66	181,00									
13	6033	I_2M	8	62	122,14	65	107,13	464,00	—	—	—	—	—	—
	1214	K	2	79	2,00									
14	6037	I_2M	7	78	10,00	81	132,57	102,00	—	—	—	—	—	—
	1221	K	39	82	151,92									
15	6038	I_2M	9	61	43,25	74	134,27	3089,00	—	—	—	—	—	—
	1222	K	8	88	238,28									
16	6039	I_2M	10	97	64,33	98	86,72	38,00	—	—	—	—	—	—
	1223	K	28	99	94,18									
17	6040	I_2M	8	73	44,14	92	213,77	3713,00	—	—	—	—	—	—
	1225	K	33	97	250,87									
18	6048	I_2M	10	105	172,44	98	319,24	815,00	—	—	—	—	—	—
	1239	K	13	93	429,33									

Group No.	Field No.	Inbreeding generation	Number of plants	Average height cm.	Variance	Average MK	var_{MK}	$var_{M/K}$	Average MI_3	var_{MI_3}	var_{M/I_3}	Average KI_3	var_{KI_3}	var_{K/I_3}
19	6049	I_2M	10	72	45,11	79	62,27	1337,00	—	—	—	—	—	—
	1240	K	7	90	88,00									
20	6054	I_2M	10	84	103,44	92	77,78	892,00	—	—	—	—	—	—
	1248	K	28	95	69,22									
21	6056	I_2M	9	77	233,25	86	157,07	1737,00	—	—	—	—	—	—
	1251	K	7	98	55,50									
22	6060	I_2M	10	65	15,67	80	99,73	3650,00	—	—	—	—	—	—
	1256	K	14	90	157,92									
23	6064	I_2M	9	80	75,62	85	116,20	342,00	—	—	—	—	—	—
	1264	K	13	88	132,23									
24	1212	K	6	88	258,40	—	—	—	—	—	—	68	108,57	3840,00
	1211	I_3	10	56	25,33									
25	1246	K	22	86	199,19	—	—	—	—	—	—	83	183,30	1170,00
	1245	I_3	3	65	16,50									
26	1253	K	11	82	114,30	—	—	—	—	—	—	75	116,75	2567,00
	1252	I_3	3	49	129,00									

therefore with certainty assume that I_2 mother clones differ from K families in height and that in 12 of these groups the K families are taller.

In comparing the average heights of the I_2 clones and of the I_3 families it will be seen that in 8 groups the I_3 families are lower and in 3 groups taller than the I_2 clones. In the twelfth group (No. 10) the height of the I_2 clone and the I_3 family is exactly the same, but the latter consists of only one individual. In 6 groups the statistical significance of the differences in height is satisfactory. In all these cases the height is lower in the I_3 families. In the other 5 groups the differences have no significance. A depression in height has therefore taken place in 6 cases after inbreeding from I_2 to I_3 but in none of the cases examined is it possible to show a significant increase.

For the purpose of comparison between K and I_3 families there are 14 groups available, all of which show the greater average in the K family. In 11 of these groups the differences are significant but in the other 3 the differences can have arisen from chance variation alone.

If we had taken the differences between the K and the I families to signify the effect of inbreeding, as was done in treating the material after the 1926 and 1927 mother plants, then it would be possible to prove the occurrence of such an effect in 11 of the 14 groups, but if we take the differences between the I_2 mother clones and the I_3 families as a measurement of the effect of inbreeding then the occurrence of such an effect from I_2 to I_3 has been shown in only 6 of the 12 groups.

In 11 groups, viz. Nos. 1—9 and 11—12, a complete comparison is possible between I_2 mother clone, K family and I_3 family. In group 1 no significant difference can be shown between mother clone and K family but the I_3 family is significantly lower than both mother clone and K family. In group 2 the K family is significantly taller than the mother clone and the I_3 family, between which no difference can be shown. In groups 3, 5 and 8 conditions are the same as in group 2, while group 4 exhibits a lower height in both K and I_3 families than in the mother clone, between

K and I_3 there is no significant difference. In group 6 the mother clone and the *K* family are of the same height, I_3 differing in having a lower height. In group 7 a significant difference can be shown only between I_2 and I_3. Groups 9 and 11

TABLE 51. *Analysis of Variance of the Height of I_3-Mother Clones, I_4-Families and K-Families in Strain No. 121. Measurements in 1931.*

Group No.	Field No.	Inbreeding generation	Number of plants	Average height cm.	Variance	Average MK	var_{MK}	$var_{M/K}$	Average MI_4	var_{MI_4}	var_{M/I_4}	Average KI_4	var_{KI_4}	var_{K/I_4}
1	6076	I_3M	8	78	203,57	96	131,54	3384,00	75	299,33	126,00	96	170,19	4248,00
	1288	K	22	102	107,52									
	1287	I_4	6	72	433,40									
2	6083	I_3M	6	51	75,60	59	203,17	1352,00	57	221,00	472,00	70	557,75	342,00
	1295	K	2	81	841,00									
	1294	I_4	4	65	463,33									
3	6087	I_3M	10	97	19,67	95	29,17	184,00	86	65,97	1785,00	82	81,64	219,00
	1300	K	4	89	57,67									
	1299	I_4	23	81	84,91									
4	6098	I_3M	3	47	37,50	77	146,88	3276,00	46	25,67	11,00	79	151,50	2706,00
	1312	K	16	83	161,47									
	1311	I_4	2	44	2,00									
5	6104	I_3M	9	67	28,00	82	82,16	2907,00	66	45,00	41,00	86	111,72	1314,00
	1321	K	18	89	107,65									
	1320	I_4	2	62	181,00									
6	1304	K	29	88	129,21	—	—	—	—	—	—	82	129,97	4116,00
	1303	I_4	12	66	131,91									
7	6081	I_3M	10	97	28,33	98	61,55	85,00	—	—	—	—	—	—
	1292	K	3	103	211,00									
8	6085	I_3M	9	66	73,75	79	72,08	3687,00	—	—	—	—	—	—
	1297	K	6	98	69,40									
9	6086	I_3M	10	73	30,11	91	41,06	6130,00	—	—	—	—	—	—
	1298	K	10	108	52,00									
10	6090	I_3M	10	64	83,33	68	70,82	748,00	—	—	—	—	—	—
	1302	K	3	82	14,50									
11	6092	I_3M	10	84	30,11	87	105,11	119,00	—	—	—	—	—	—
	1304	K	29	88	129,21									
12	6100	I_3M	5	87	159,75	89	116,18	28,00	—	—	—	—	—	—
	1314	K	8	90	91,29									
13	6101	I_3M	10	79	29,00	87	72,05	990,00	—	—	—	—	—	—
	1316	K	14	92	101,85									
14	6102	I_3M	10	89	13,00	92	93,17	414,00	—	—	—	—	—	—
	1318	K	4	101	333,67									
15	6103	I_3M	7	49	38,33	57	33,57	2130,00	—	—	—	—	—	—
	1319	K	2	86	5,00									

exhibit significant differences in all comparisons, therefore *K* is taller than I_2 and I_3, and I_3 is lower than I_2. In group 12, on the contrary, no differences can be shown. Thus, the height is equal in the I_2 mother clone and in the two progeny families only in the last-mentioned group. Of the other groups an effect of continued inbreeding was ascertained in Nos. 1, 4, 6, 8, 9 and 11, while simultaneously in free

flowering a previously occurring inbreeding effect has been annulled more or less in groups 9 and 11. In group 4 a significant depression has also occurred in *K*, and I_2 is taller than the *K* family. In groups 2, 3, 5 and 8 no inbreeding effect has been brought about from I_2 to I_3 but in *K* a luxuriance was ascertained.

From the summarizing analysis of variance given in Table 52 it appears that the variation within the *K* families and within the I_3 families is greater than the variation within the mother clones. The difference between *K* and I_2 is significant but insignificant between I_3 and I_2, which signifies that the variation between the plants within the families is partly caused by an hereditary differentiation between the plants, which is evident in the *K* material. There is also a pronounced differentiation in height between the clones and between the families in the *K* and I_3 material, this differentiation being apparent from the great differences between the interclass and intraclass variances in all the comparisons. It is worthy of note, however, that the differentiation is greater between the I_2 clones than between the families in the *K* and the I_3 material. There is a statistical significance for this inequality in the differentiation. On the average the height is greatest in the *K* families, lowest in the I_3 families, and the I_2 mother plants occupy an intermediate position.

The classification into different groups presented in Table 52 shows that taken on the average there is a very pronounced differentiation between mother clones and *K* families, between mother clones and I_3 families and between *K* families and I_3 families. This differentiation is greatest between *K* families and I_3 families and lowest between I_2 clones and I_3 families, and the differences are significant. The reason for this is that in comparison with the mother clones an average increase has occurred in the *K* families and the I_3 families exhibit an average depression in height, thus the groups of the *K* and I_3 material differ from each other more than they do severally from the mother plants. Further, it is evident from the groups formed of I_2 clones and *K* families, I_2 clones and I_3 families and *K* and I_3 families that in each kind of grouping there is a marked differentiation between the groups, as the variation in all cases is considerably greater betwen the groups than within them and the differences are statistically significant. This differentiation is greatest between groups of I_2 clones and I_3 families and lowest between groups of *K* and I_3 families, but the difference is not significant. This indicates nevertheless that I_2 and I_3 are more closely related to each other than *K* and I_3, which was already seen in the discussion on the individual mother clones and their progeny families.

TABLE 52. *Summarizing Analysis of Variance of the Height in Strain No. 121. Measurements in 1931.*

	Average height cm.	Number			Σd^2	D. F.	Variance
		Plants	Families	Groups			
I_2-mother clones with progeny							
I_2-mother clones	82	113	12	—	—	—	—
Within clones	—	—	—	—	10797,00	101	106,90
Between »	—	—	—	—	24374,00	11	2215,82
Total	—	—	—	—	35171,00	112	314,03
K-families	91	250	12	—	—	—	—
Within families	—	—	—	—	33083,00	238	139,00
Between »	—	—	—	—	8337,00	11	757,91
Total	—	—	—	—	41420,00	249	166,35
I_3-families	75	85	12	—	—	—	—
Within families	—	—	—	—	9107,00	73	124,75
Between »	—	—	—	—	8072,00	11	733,82
Total	—	—	—	—	17179,00	84	204,51
In Groups							
I_2-mother clones and K-families	88	655	46	23	—	—	—
Within clones and fam. within groups	—	—	—	—	81198,00	609	133,33
Between clones and fam. within gr.	—	—	—	—	30967,00	23	1346,39
Total within groups ...	—	—	—	—	112165,00	632	177,48
Between groups	—	—	—	—	43630,00	22	1983,18
Total	—	—	—	—	155795,00	654	238,22
I_2-mother clones and I_3-families	79	198	24	12	—	—	—
Within clones and fam. within groups	—	—	—	—	19904,00	174	114,39
Between clones and fam. within groups ...	—	—	—	—	8790,00	12	732,50
Total within groups ...	—	—	—	—	28694,00	186	154,27
Between groups	—	—	—	—	25841,00	11	2349,18
Total	—	—	—	—	54535,00	197	276,83
K- and I_3-families	85	376	28	14	—	—	—
Within families within groups	—	—	—	—	42344,00	348	121,68
Between families within groups	—	—	—	—	28717,00	14	2051,21
Total within groups ...	—	—	—	—	71061,00	362	196,30
Between groups	—	—	—	—	16640,00	13	1280,00
Total	—	—	—	—	87701,00	375	233,87

	Average height cm.	Number			Σd^2	D. F.	Variance
		Plants	Families	Groups			
I_3-mother clones with progeny							
I_3-mother clones	73	36	5	—	—	—	—
Within clones	—	—	—	—	2279,00	31	73,52
Between »	—	—	—	—	12216,00	4	3054,00
Total	—	—	—	—	14495,00	35	414,14
K-families	92	62	5	—	—	—	—
Within families	—	—	—	—	7524,00	57	132,00
Between »	—	—	—	—	3936,00	4	984,00
Total	—	—	—	—	11460,00	61	187,87
I_4-families	75	37	5	—	—	—	—
Within families	—	—	—	—	5608,00	32	175,25
Betwen »	—	—	—	—	3542,00	4	885,50
Total	—	—	—	—	9150,00	36	254,17
In Groups							
I_3-mother clones and K-families	85	258	28	14	—	—	—
Within clones and fam. within groups	—	—	—	—	21040,00	230	91,48
Between clones and fam. within groups ...	—	—	—	—	25434,00	14	1816,71
Total within groups ...	—	—	—	—	46474,00	244	190,47
Between groups	—	—	—	—	27313,00	13	2101,00
Total	—	—	—	—	73787,00	257	287,11
I_3-mother clones and I_4-families	74	73	10	5	—	—	—
Within clones and fam. within groups	—	—	—	—	7887,00	63	125,19
Between clones and fam. within groups ...	—	—	—	—	2435,00	5	487,00
Total within groups ...	—	—	—	—	10322,00	68	151,79
Between groups	—	—	—	—	12280,00	4	3070,00
Total	—	—	—	—	22602,00	72	313,92
K- and I_4-families	84	140	12	6	—	—	—
Within families within groups	—	—	—	—	18199,00	128	142,18
Between families within groups	—	—	—	—	12945,00	6	2157,50
Total within groups ...	—	—	—	—	31144,00	134	232,42
Between groups	—	—	—	—	6010,00	5	1202,00
Total	—	—	—	—	37154,00	139	267,29

From Table 51, which contains an analysis of the variation in I_3 mother clones and their derivative K and I_4 families, it will be seen that there are 14 possible comparisons between I_3 clones and K families. In 13 of them the K families have the greatest height and in only one instance is the height lower in the K family than in the mother clone. In this last instance a depression has therefore occurred in K and the difference is significant. In the groups showing an increase in height in the K families the differences are significant in 9 of them but not in the remaining 4. Thus, in 9 cases out of 14 free flowering has given rise to a luxuriation of the height as compared with the mother clones.

Only 5 comparisons are possible between I_3 mother clones and I_4 families, and only in one of these cases can any difference in height be shown for certain, in this case I_4 being lower than I_3. In 3 of the 6 comparisons between K and I_4 families it can be shown that I_4 is lower than the K families but in the other 3 there is no significant difference in height.

Groups 1—5 consist of I_3 clones as well as K and I_4 families and in these groups a complete comparison is possible. These comparisons show that in group 1 a significant increase has taken place in K, I_3 and I_4 are equal and between K and I_4 there is a significant difference. Group 2 exhibits a significant difference only between K and I_3 with an increase in K. Group 3 shows a decrease in height between I_3 on the one hand and K and I_4 on the other hand, no significant difference existing between K and I_4. Groups 4 and 5 indicate a significant increase in K, no significant change in the height after continued inbreeding but a significant difference between the K and the I_4 families.

Free flowering has therefore brought about an increase in height in 4 cases and a depression in the 5th case, while continued inbreeding from I_3 to I_4 has caused a significant depression in only 1 case out of 5.

The summarizing analysis of variance in I_3 mother plants and their progenies presented in Table 52 shows a greater intraclass variance in the K and I_4 material than in the I_3 material. The difference between I_4 and I_3 is significant but insignificant between K and I_4. The differentiation between the clones in the I_3 material and between the families in the K and the I_4 materials is positively demonstrable. As evidenced by the table this differentiation is, however, less between the K and the I_4 families than between the I_3 clones. Although the differences between these groups are not significant they are nevertheless suggestive.

The division into groups presented in Table 52 shows on the average a pronounced differentiation between clones and progeny families and also between K families and I_4 families. This differentiation is greatest between K families and I_4 families and least between I_3 clones and I_4 families. Between the groups the conditions are just the reverse, the greatest differentiation being between groups of I_3 and I_4 and least between groups of K and I_4 families, which might have been expected

to be the case from the results obtained in comparisons between the individual mother plants and their progenies in *K* and I_4 families.

Finnish timothy. — The material of *Finnish* timothy consists of I_3 mother clones and their derivatives after free flowering and one family after isolation.

The analysis of variance in mother clones and *K* families is found in Table 53, in which is seen that in 6 cases out of 7 the *K* families are on the average taller than the I_3 mother plants, but the differences are significant in only 4 of these groups.

TABLE 53. *Analysis of Variance of I_3 Mother Plants and K-Families after Them. Finnish Timothy. Measurements in 1931.*

Group No.	Field No.	Inbreeding generation	Number of plants	Average height cm.	Variance σ^2	Group average cm.	var_{ab}	var_p
1	6114	I_3M	10	63	41,44	72	52,00	1778,00
	1338	*K*	8	83	65,57			
2	6115	I_3M	7	59	308,33	61	320,28	78,00
	1339	*K*	2	66	392,00			
3	6116	I_3M	10	51	13,89	59	33,27	2827,00
	1340	*K*	3	86	65,50			
4	6117	I_3M	8	73	111,71	76	221,80	108,00
	1342	*K*	9	78	318,12			
5	6118	I_3M	10	78	32,11	83	60,21	544,00
	1344	*K*	6	90	110,80			
6	6119	I_3M	10	96	18,78	92	169,37	184,00
	1346	*K*	24	91	228,30			
7	6123	I_3M	10	86	46,33	96	128,37	1128,00
	1349	*K*	32	98	152,19			

The I_4 family grown after isolation of the I_3 mother plant 6117, which should be compared on the one hand with the mother plant and on the other hand with *K* family No. 1342, has not been included in the table. The average height of the 17 individuals found of this family amounts to 64 cm. (variance 45,81) and is less than the mean height of both the I_3 mother clone and the *K* family. Statistically significant differences exist between I_3 clone and I_4 family and also between *K* family and I_4 family and the I_4 family is therefore lower than the I_3 clone and *K* family. The difference between the I_3 clone and the *K* family is not significant. In this group inbreeding from I_3 to I_4 has therefore caused a depression but no luxuriation has been caused in free flowering.

Table 54 gives a summarizing analysis of variance in the I_3 mother plants and the *K* families of *Finnish* timothy. A comparison between the I_3 material and the *K* material will show that the variation is greater within the *K* material than within the I_3 material, the difference being

statistically significant. On the other hand, the interclass variance is greater in the I_3 material than in the *K* material and this signifies that the differentiation between the mother plants has been diminished in the *K* families. Though the difference between the interclass variances is not significant it is nevertheless suggestive. Within both groups the interclass variance is significantly greater than the intraclass variance,

TABLE 54. *Summarizing Analysis of Variance of the Height of Finnish Timothy in 1931.*

	Average height cm.	Number			Σd^2	D. F.	Variance
		Plants	Families	Groups			
I_3-mother clones	73	65	7	—	—	—	—
Within clones	—	—	—	—	4005,00	58	69,05
Between »	—	—	—	—	14442,00	6	2407,00
Total	—	—	—	—	18447,00	64	288,23
K-families	91	84	7	—	—	—	—
Within families	—	—	—	—	14050,00	77	182,47
Between »	—	—	—	—	3732,00	6	622,00
Total	—	—	—	—	17782,00	83	214,24
I_3-mother clones and K-families in groups	83	149	14	7	—	—	—
Within clones and fam. within groups	—	—	—	—	18055,00	135	133,74
Between clones and fam. within gr.	—	—	—	—	6647,00	7	949,57
Total within groups	—	—	—	—	24702,00	142	173,96
Between groups	—	—	—	—	24707,00	6	4117,83
Total	—	—	—	—	49409,00	148	333,84

which indicates a differentiation in both the I_3 material and the *K* material.

The analysis of variance in a group arrangement of the material exhibits in the first place a differentiation between I_3 clones and *K* families, in which the latter are taller, and in the second place that the groups consist of well differentiated height-populations, as the inter-group variation is significantly greater than the total intra-group variation.

Kämpe timothy. — The *Kämpe* strain is represented in the 1931 material by the original *Kämpe* population and by three I_3 mother plants with their progenies, in addition to which the plants of family

4933 selected in 1929 are included along with progenies produced after free flowering.

Table 55 contains the mean heights of the *Kämpe* population, three I_3 mother plants, one I_4 family and three *K* families. Unfortunately, the number of plants in

TABLE 55. *Analysis of Variance of Height in the Kämpe Strain. Isolations in 1929. Measurements in 1931.*

Group No.	Field No.	Inbreeding generation	Number of plants	Average height	σ^2	
	1359	I_0	18	94	149,24	The original Kämpe strain
1	5511	I_3M	8	87	7,00	
	1201	I_4	4	47	37,00	
	1202	K	2	24	50,00	
2	5514	I_3M	3	28	61,00	
	1203	K	1	74	—	
3	5516	I_3M	8	65	22,29	
	1204	K	7	43	—	

TABLE 56. *Analysis of Variance of I_1-Mother Clones and K-Families after Them. Family No. 4933 from Kämpe. Measurements in 1931.*

Group No.	Field No.	Inbreeding generation	Number of plants	Average height cm.	Variance	Group average cm.	$Var._{ab}$	$Var._p$
1	5880	I_1M	2	80	18,00	98	228,10	808,00
	1324	K	10	102	251,44			
2	5883	I_1M	2	102	18,00	108	208,16	36,00
	1325	K	31	108	214,50			
3	5885	I_1M	2	39	200,00	62	200,00	2994,00
	1326	K	1	108	—			
4	5892	I_1M	2	65	2,00	92	97,57	1906,00
	1327	K	7	100	113,50			
5	5908	I_1M	2	51	18,00	96	112,75	4638,00
	1331	K	12	103	121,36			
6	5934	I_1M	2	59	145,00	80	149,60	1202,00
	1334	K	5	88	150,75			

each family is too small for a reliable complete analysis of variance, still there is some evidence which suggests that the original *Kämpe* population is taller than I_3 plants, I_4 families and *K* families. The 4 individuals in the I_4 family show a considerably lower average height than their mother clone and the same thing is true of the 2 individuals from the same mother plant after free flowering. Free flowering does not therefore seem to have caused any luxuriation.

The I_1 mother plants selected from family 4933 and their progeny plants after free flowering have been grouped together in Table 56. The *K* families seem on the whole to be taller than their mother plants and it might therefore be assumed that free flowering has entirely or partially suspended the depression in I_1. The small number of individuals does not permit of the differences in height being shown statistically except in the last three groups in the table. There is also a certain probability that an increase has taken place in the other groups after free fertiliza-

TABLE 57. *Analysis of Variance of the Height of I_0-Mother Clones and I_1- and K-Families after Them. Russian Timothy. Measurements in 1931.*

Group No.	Field No.	Inbreeding generation	Number of Plants	Average Height cm.	σ^2	Average MI	$Var._{MI}$	$Var._{M/I}$	Average MK	$Var._{MK}$	$Var._{M/K}$
1	6066	I_0M	6	73	199,20	—	—	—	70	255,06	66,00
	1269	I_1	1	74	—						
	1270	K	12	69	280,45						
2	6067	I_0M	10	81	37,00	—	—	—	86	100,31	439,00
	1272	K	21	89	128,80						
3	6068	I_0M	9	73	44,12	—	—	—	71	86,71	50,00
	1273	K	14	70	112,92						
4	1274	I_1	1	65	—						
	1275	K	13	68	167,58						
5	6069	I_0M	10	64	31,78	—	—	—	72	147,97	874,00
	1276	I_1	1	63	—						
	1277	K	26	75	189,80						
6	6070	I_0M	10	84	24,22	72	70,67	2493,00			
	1278	I_1	13	63	105,50						
	1279	K	1	48	—						
7	6071	I_0M	10	69	1,44	70	4,45	28,00	72	1,30	128,00
	1280	I_1	2	73	32,00						
	1281	K	2	79	0						
8	6072	I_0M	10	76	96,89	73	95,00	282,00	80	190,72	313,00
	1282	I_1	3	65	86,50						
	1283	K	17	83	243,50						

tion, as low mother plants when flowering were surrounded by tall types which might have been the fathers of the progenies and have transmitted to them a greater height or a greater degree of vegetative vigour.

Russian timothy. — In *Russian* timothy seven I_0 mother clones, six I_1 families and eight *K* families were analysed.

The groupings in Table 57 show that the number of plants in most of the families is too small to give significant results of the analysis of variance. From the magnitude of the interclass and intraclass variances in the groups of I_0 clones and of I_1 families it is still possible to assume that an inbreeding effect has taken place in one I_1 family, in another family an increase in height is discernible, but the small number of plants does not permit of any definite conclusion being drawn

on this point. A significant increase can be shown between I_0 clones and *K* families in 3 groups, but no significant difference is obtained in the other groups. It is of interest to note that an increase has occurred in *K* families although no inbreeding has taken place previously. The selected mother plants are, however, low and have evidently been crossed with taller types so that a progeny has been produced having a greater average height than the mother plants. No significant differences can be shown between the I_1 and the *K* families.

Analysis of variance of inbreeding effect in height in strain 121. — According to the above account the material analysed in 1931 seems to indicate that inbreeding frequently brings about a depression in the height of the progeny both in comparison with mother clones and in comparison with *K* progenies grown simultaneously. The differences apparent in these two kinds of comparisons occasionally run parallelly, but frequently they point in opposite directions. It is therefore a matter of interest to analyse more closely the inbreeding effects found so as to form a definite conception of what should be called inbreeding effect and how great this effect is.

Unfortunately, owing to the available material of all the strains examined being insufficient the analysis of variance of the magnitude of the inbreeding effect has to be limited to strain *121*, in which a number of comparisons are possible, partly on material inbred from I_2 to I_3 and partly on material inbred from I_3 and I_4. For this analysis, however, it was only possible to include such mother plants as had produced, in addition to clone material, both *K* and *I* families. Eleven such complete groups are found with inbreeding from I_2 to I_3 and five with inbreeding from I_3 to I_4. In these groups comparisons were made between mother clones and *I* progeny and between *K* and *I* progenies. From Table 58 it is seen that the inbreeding effect is greatest in comparisons between *K* and *I* families after both I_2 and I_3 mother plants. The inbreeding effect between I_2 clones and I_3 families derived from them is on the average 10,2 cm. while the average difference between *K* and I_3 families amounts to 17,2 cm. In both cases the interclass variance of inbreeding effect is decidedly greater than the intraclass variance and the differences are significant. From this we should be justified in assuming that the effect of inbreeding really differs after separate mother plants, whether the effect is determined in one way or the other. There is only a slight insignificant difference between the two interclass variances.

Between the two different values of the inbreeding effect in the same I_3 family there is, however, a rather great difference. Between these values a marked interclass variance is also obtained, amounting

to 1149,25, while the total intraclass variance is only 133,65. The differences between them has great statistical significance, thus no doubt proving that the inbreeding effects on the same inbred material determined in different ways are unequal.

The average inbreeding effect between I_3 clones and I_4 families is 7,1 cm. and between K families and I_4 families 23,7 cm. In both cases the interclass variance of inbreeding effect is statistically greater than the intraclass variance, which signifies that even in inbreeding from

TABLE 58. *Analysis of Variance of the Inbreeding Effect in Height in Strain No. 121.*

	Number of groups	$\Sigma\left(\frac{n_1 n_2}{n_1 + n_2}\right)$	Inbreeding effect cm.	Σd^2	D. F.	Variance
Between I_2-clones and I_3-families	11	40,0	10,2			
Intraclass	—	—	—	19063,00	166	114,84
Interclass	—	—	—	4638,20	10	463,82
Between K-families and I_3-families	11	56,7	17,2			
Intraclass	—	—	—	37907,00	299	126,78
Interclass	—	—	—	4200,81	10	420,08
Between I_3-clones and I_4-families	5	15,6	7,1			
Intraclass	—	—	—	7887,00	63	125,19
Interclass	—	—	—	1654,32	4	413,58
Between K-families and I_4-families	5	13,0	23,7			
Intraclass	—	—	—	13132,00	89	147,55
Interclass	—	—	—	1542,65	4	385,66

I_3 to I_4 the inbreeding effect is certainly different after different mother plants. Between the intraclass and interclass variances in the inbreeding effects determined in different ways there are only minor differences without any statistical significance. The different values of the inbreeding effect, however, differ widely. The difference also has great statistical significance and it can therefore be established that entirely different values of the inbreeding effect are obtained, when I_3 and I_4 or when K and I_4 are compared.

After finding that the inbreeding effect from I_2 to I_3 is 10,2 cm. or 17,2 and from I_3 to I_4 7,1 or 23,7 cm. we shall examine if any inequality occurs in the effect between the different generations. The inbreeding effect found between mother plants and inbred progenies averages

9,3 cm. in the two generations. The interclass variance amounts to 107,90 (D. F. = 1) and the total intraclass variance is 136,24 (D. F. = 244). Since the intraclass variance is therefore the greater no difference can be shown to exist. Neither can any significant difference be shown between the inbreeding effect in the different inbreeding generations, when the effect is determined by the differences between *K* and *I* families. In this case the interclass variance will be greater than the intraclass variance, but the difference has no statistical significance.

No significant correlations could be found between the magnitude of the inbreeding effect and the variance in *I*, whether in inbreeding from I_2 to I_3 or from I_3 to I_4.

c) REVIEW OF THE RESULTS.

Fertility.

A large number of isolations have been made on plants belonging to the tall hay-type of timothy grass. On an average the seed setting was very low upon isolation, but a very wide variation occurred, including completely »self-sterile» plants as well as highly self-fertile ones. Of 121 plants, isolated in 1927, 19 % did not give any seed at all. The most fertile plant in this year gave, in an average of 12 panicles isolated, 521 seeds per panicle, which is calculated to be about 46 % of the number of florets. On the same plant the highest value for a single panicle was obtained, viz. 602 seeds. In 1929 the highest values for single panicles were 992 and 692 seeds, corresponding to 143,8 and 104,8 seeds per panicle cm. respectively. In 1930 the highest single panicle values were 760 and 745 seeds, or 106,4 and 86,4, respectively, per cm. Thus, the highest single panicle value was obtained in 1929.

In 1929 and 1930 a small number of plants of the *nodosum*-variety have been isolated, and this type has been found to be less »self-fertile» than the tall type. In 1929 4 out of 5 isolated plants did not give any seed at all, on the fifth plant one seed was obtained from 5 isolated panicles. In 1930 the number of seeds per panicle varied between 0 and 23,7 in the different isolated plants.

The seed setting on isolation is different in different years. Only a few plants have been isolated more than one year, however, and therefore it has not been possible to demonstrate a significant difference between the amount of seed setting in different years. There is a fairly good agreement between the different years as regards the relative

amount of seed obtained from different isolated plants. 5 plants were isolated in 1927 and 1929. All of them showed a reasonable »self-fertility», and the correlation coefficient between the number of seeds in the two years was + 0,58. 9 plants were isolated in 1928 and 1929. Of these 6 plants were completely »self-sterile» in both years, 1 was »self-sterile» in 1928 and very weakly fertile in 1929, 2 plants, finally, gave in both years a very small amount of seed upon isolation. Also between the results of isolations made on the same plants in 1929 and 1930 there was a good agreement.

Different commercial strains of timothy, as represented in the material, have given different averages of »self-fertility», and these differences have been observed in each year of the investigations. The difference between *Kämpe* and strain *121* is especially striking. *Kämpe* seems to contain a majority of »self-sterile» or very weakly self-fertile biotypes, whereas strain *121* includes highly self-fertile biotypes, as well as some »self-sterile» or nearly sterile types.

In a couple of cases the material offers a possibility of comparing different *I* generations of the same strain as regards isolation-fertility, but no definite effect of prolonged inbreeding upon the average isolation-fertility can be demonstrated. In one case the seed setting is lowest in the most inbred generation, in another case, however, the reverse condition is found. The most inbred generations are not, however, derived from the less inbred generations investigated, but the different generations represent different selections in the original populations. No conclusions as regards the effect of inbreeding upon isolation-fertility may, therefore, be drawn from this comparison, and the differences in fertility found are probably due to chance differences in the selected material. If the average isolation-fertility of inbred progenies is compared with the isolation-fertility of the respective mother plants, no average decrease in fertility is observed.

There is a good agreement between the isolation-fertility of the individual plant and the mean isolation-fertility of its inbred progeny, and this fact holds true for plants isolated in 1926 as well as in 1927. There is a correlation of + 0,64 between the isolation-fertility of 29 plants, isolated in 1927, and the mean isolation-fertility of their progenies in 1930. It has thus been possible to demonstrate a comparatively strong inheritance of different degrees of isolation-fertility.

The heritable nature of the differences in isolation-fertility is further proved by the large differences between inbred families in this respect. Some families have turned out nearly sterile or completely so upon

isolation, as far as may be concluded from the plants investigated. Other families show a good fertility in all plants. One I_3 family of strain *121* had a very good fertility, the average of all plants investigated being 218,8 seeds per panicle. The mother plant of this family was isolated in 1927 and gave 306,1 seeds per panicle. This seems to be a case of constant high isolation-fertility, whereas other families present cases of constant low fertility. In most families the individuals are widely differentiated, such families comprise nearly or completely sterile plants as well as rather highly fertile ones. No instance of an apparently constant intermediate degree of isolation-fertility has occurred. One I_1 family of *Kämpe* was closely investigated in 1930 and showed a very wide variation in fertility as well as in morphological characters. Of 64 isolated plants in this family 15 were completely »self-sterile», whereas the others varied between 0,1 and 38,7 seed per panicle cm.

The seed setting upon open flowering was investigated in 1927 and 1929, the last year giving on an average the highest amount of seed. In both years there is a very wide variation in seed setting. 10 plants, sterile upon isolation, were equally sterile when openly pollinated. The average amount of seed in fertile plants in 1927 was 261,4 seeds per panicle, whereas the same plants gave only 24,0 seeds per panicle upon isolation. Thus, in this year the isolation-fertility was on an average only 9,2 % of the general fertility. The maximum number of seeds per panicle upon open flowering was in 1927 551,8 (about 52 % of the flowers), in 1929 1246,3 (about 85 % of the flowers). The figures are not, however, directly comparable, since they refer to different plants in the different years.

There are great differences between different plants as regards the seed setting on open flowering. The differentiation is more marked, however, in respect to isolation-fertility than as regards general fertility. The differences between different isolated panicles on the same plant are also greater than between openly pollinated panicles on the same plant.

There is a very significant correlation between the amount of seed setting on isolation and the general fertility on open flowering. In 1927 the coefficient of correlation is $+ 0{,}72$ (18 plants), in 1929 it is $+ 0{,}41$ (98 plants), in both cases the completely sterile plants are excluded from the calculation of the correlation.

If that variation in isolation-fertility, which is correlated with the variation in general fertility, is eliminated, there still remains a varia-

tion in isolation-fertility between plants, which is significantly larger than the variation between panicles on the same plant. This indicates that there is a genetic variation in isolation-fertility, independent of general fertility.

The *nodosum*-variety is less fertile on open flowering than the tall type.

Inbreeding effects.

The effect of isolation upon the development of the seed has been studied only in 1929. This year the germination of isolated seed as well as of seed after open pollination of the same plant was determined. The average germination percentage of isolated seed from 39 plants was 80,4 %, whereas non-isolated seed from the same plants showed an average germination of 74,7 %. The difference is not significant, but neither does it indicate any detrimental influence of the isolating methods used upon the development of the seed. The variation in germination percentage is greater in the isolated seed than in the non-isolated, but the difference is insignificant. Between germination percentages of isolated and non-isolated seed from the same mother plant there is a significant positive correlation, $r = + 0{,}57$.

Chlorophyll-deficient seedlings are rather numerous in many families, *I* families (inbred) as well as *K* families (after open pollination). Besides pure *albino* seedlings there occur yellow and yellowish green ones. In some families the segregation is probably monofactorial, in other cases it is decidedly more complicated. A couple of cases have been observed with white (chlorophyll-less) panicles. In the progeny after one I_2 plant with white panicles there occurred normals and white panicles in a ratio approaching 1 : 2. This indicates that the white panicle should be the effect of a lethal factor in a heterozygous state. Chlorophyll-deficient seedlings in *K* material are more frequent after highly inbred mother plants than after less inbred ones.

A very wide differentiation between individual plants of the same progeny has been observed in regard to several characters, such as height, panicle-length, tillering, leafiness and winter-hardiness. This differentiation is in general more marked after isolation than after free flowering. Sterile types have been observed in some families, viz. plants without fertile straws or plants with abnormal panicles, lacking normally developed sexual organs.

Great differences in winter-hardiness between *I* and *K* material were observed in 1929. 39 groups of *I* and *K* progenies from the same

mother plant were sown in 1927. In 1929 15,5 % of the plants had died in the *I* families, the average mortality of the *K* families was only 1,6 %. In material sown in 1928 the mortality was on an average 6,3 % in the inbred families but only 0,7 % in the corresponding families after open pollination. The differences between different families as regards mortality are in both cases significantly larger in the *I* material than in the *K* material. In two more closely examined pairs of families (I_3 and *K* from the same mother plant) the mortality was 27,2 % and 45,9 % in the I_3 families, 3,3 % and 6,9 % in the respective *K* families. In some cases a high rate of mortality occurs in families with chlorophyll-deficient seedlings, in other cases no such deficiencies are combined with the high mortality. No correlation can be demonstrated between mortality in *I* and *K* progenies after the same mother plant.

In two pairs of I_3 and *K* families the tillering has been more accurately measured. In both cases it was significantly poorer in I_3 than in *K*.

In the same material the panicle length is significantly lower in I_3 than in *K*.

In 114 cases the mean height of an *I* family (I_1, I_2, I_3 and I_4) is compared with the mean height of the *K* family from the same mother plant. The results are summarized in the table below.

	I significantly lower than *K*	No significant difference	*I* significantly taller than *K*
I_1 compared with *K*	30	14	3
I_2 » » *K*	13	1	—
I_3 » » *K*	36	11	—
I_4 » » *K*	3	3	—

In several cases in 1931 it has been possible to compare directly the height of the sexual progenies with the height of the vegetatively propagated mother plant. The comparisons between *I* and *K* progenies and the mother-clone are summarized below.

	K significantly taller than mother clone	No significant difference	*K* significantly lower than mother clone
I_0-clone compared with *K*	3	4	—
I_1- » » » *K*	3	3	—
I_2- » » » *K*	12	11	1
I_3- » » » *K*	18	9	1

	I significantly lower than mother clone	No significant difference	*I* significantly taller than mother clone
I_1 compared with I_0-clone	3	8	—
I_3 » » I_2- »	6	5	—
I_4 » » I_3- »	1	4	—

Finally, the cases where comparisons between mother clone, *K* and *I* were possible are summarized as follows (cl = mother clone): —

	$K > \text{cl} > I$	$K > \text{cl} = I$	$K = \text{cl} > I$	$K = \text{cl} = I$	$\text{cl} > K = I$
I_0—I_1	—	—	1	3	1
I_2—I_3	2	4	2	1	2
I_3—I_4	—	4	1	—	2

If a total average is taken, the inbred progenies are significantly lower than *K* progenies, and the mother clones are intermediate. On an average mother clone and *I* family differ less in height than either one of them differs from *K* family. The significant average difference between *I* and *K* is found not only when all the material is taken together, but also within smaller groups of material such as all material in a year, all material of a certain strain, all material of a certain generation.

On the other hand, the effect of inbreeding upon height differs greatly after different isolated mother plants, and these differences are significant. This differentiation between mother plants as regards the effect of inbreeding upon their progeny is found within each separate year and also within each separate strain. Also, the differentiation is apparent whether the effect of inbreeding is measured by the difference between *K* and *I* or by the difference between mother clone and *I*. The average inbreeding effect is different in different strains, as represented in this material. No significant differences between the inbreeding effects in successive inbred generations can be demonstrated in the material.

Different *I* families within the same strain are widely and significantly different in regard to mean height. The same holds true of different *K* families within the same strain. The *I* progenies of plants isolated in 1926 are significantly more differentiated than the *K* progenies of the same plants. Among the progenies of plants isolated in 1927 no such differences in the degree of differentiation can be demonstrated between *K* and *I*.

In the material of 1931 a comparison is possible between *I*, *K* and mother clones. Here the mother clones differ significantly more

than the mean heights of *K* as well as *I* progenies. This holds true when the mother plants belong to I_2 as well as when they belong to I_3. Here, thus, sexual reproduction, selfing as well as open pollination, has decreased the differences existing between the mother plants.

If the *I* and *K* progenies of the same mother plant are combined, there is again a strong differentiation between the mean heights of the groups thus constituted. Also there is a marked correlation between the mean heights of the two progenies within such a group. It is thus possible to demonstrate the great influence of the genetic constitution of the mother plant, not only upon the inbred progeny, but also upon the progeny after open flowering. Even when groups are made out of *I* and *K*, *I* and mother clone or *K* and mother clone in the material of 1931, the differentiation between the group-means is significant.

Different commercial strains represent different height populations. Strain *404*, which represents an I_2 generation derived from *Kämpe* (I_0) is decidedly lower than the latter strain. On the other hand, comparative yield trials have shown that *404* yields considerably more green matter than *Kämpe*. This furnishes an example of the fact that decrease in height is not always accompanied by decrease in general vigour.

Progenies after different mother plants are also widely different as regards panicle length. There is a significant positive correlation, $r = + 0{,}67$, between the panicle length of mother plant and progeny. In two cases, where this character has been more thoroughly studied, the panicle is significantly shorter in *I* than in *K*. A decrease in panicle length in inbred progenies, as compared with the mother plants, could not be demonstrated.

In most cases the variability is greater within the inbred families than within the corresponding progenies after open pollination. In respect to height this difference in variability between *I* and *K* could be demonstrated with great statistical significance. *I* families and *K* families both have a greater variability than the corresponding mother clones.

Length of panicle and tillering also vary widely within the families. The degree of differentiation between individual plants as regards panicle length is different in different families, probably due to different degrees of heterozygosity in the mother plants. Two cases were more closely analysed. In one case the differentiation is the same within the *I* family and the corresponding *K* family, in the other case *I* is less differentiated than *K*.

The correlation between inbreeding effect in height (as measured by the difference *K*—*I*) and variability in *I* has been examined. The coefficients obtained are widely different in different strains, none of them is significant, neither are their differences. Even if the material is combined and an average correlation coefficient is calculated, this is without any significance.

In one inbred family all the plants have been vegetatively propagated. The variation between the mean heights of the clones is significantly greater than between the plantlets within the clones. Measurements of height and panicle length in this material have been made in two different years. The values in the different years are significantly correlated, $r = + 0{,}69$ and $+ 0{,}66$ respectively. If the correlated variation is eliminated, there still exists a variation between clone-means, which is significantly greater than that within the clones.

No correlation between panicle length and isolation-fertility could be demonstrated in the material investigated in 1927.

In 1929 a significant correlation could be demonstrated between height and panicle length ($r = + 0{,}56$) as well as between height and general fertility ($r = + 0{,}57$). There is probably also a genetical variation in panicle length and in general fertility, which is independent of the height, although the existence of this independent variation could not be statistically proved.

In the two pairs of I_3 and *K*, already mentioned, which were investigated in detail, positive correlations existed between height and panicle length as well as between height and tillering. In one of the groups the correlation between height and tillering is significantly stronger in the *I* family than in the *K* family. The direct correlations between panicle length and tillering are different in the two groups. If the partial correlation between these two latter characters is determined, by eliminating that part of the variation in both which is positively correlated with height, rather varying results are obtained. In the *I* family of one group there is a significant negative partial correlation, in the *K* family of the other group the partial correlation is significantly positive. In the two other families no significant correlation can be shown.

In one I_1 family with great variation in different characters several correlations have been calculated. Significant positive correlations exist between height on one hand and general fertility, isolation-fertility, panicle length, and tillering on the other. An independent genetical variation in isolation-fertility is strongly suggested by the analysis of

variance of this character. An equally independent genetical variation in panicle length is also probable, but not possible to prove. As regards the existence of independent variation in tillering and general fertility the material offers no possibilities for judging. If that part of variation in panicle length and tillering which is correlated with height is eliminated, these characters are independent of one another.

The skewness of the distributions has been determined in some cases. *I* as well as *K* progenies of I_0 plants of Swedish *Common Commercial* timothy show a weak and insignificant skewness, and there is no difference between *I* and *K*. There is a suggestive positive correlation, however, between the skewness of *I* and *K* progenies from the same mother plant. In progenies after I_1 plants of strain *121* there is a more marked negative skewness, significant in *I* progenies and rather suggestive in *K* progenies. The values of skewness are higher in I_2 than in *K*, but the difference is not significant. In this material the positive correlation between the skewness in an I_2 family and in the corresponding *K* family is significant. In progenies after I_2 plants of strain *121* the negative skewness is still more marked, significant in *I* as well as in *K*, greater in *I* with a significant difference. It is thus apparent, that the negative skewness increases with increased inbreeding, and at the same time the difference between *I* and *K* progenies becomes more marked. At the same time the variation between progenies from different mother plants, as regards skewness, increases with increased inbreeding. This differentiation between different progenies is more marked in *I* progenies than in *K* progenies. The difference between *I* and *K* families as regards skewness, and the difference between the same families as regards mean height (*i. e.* »inbreeding effect»), have been correlated. In the progeny of I_1 plants there is a suggestive negative correlation, but as no correlation is found in the other groups of material this is probably only a chance occurrence.

4. REVIEW OF RESULTS IN OTHER GRASS SPECIES.

a) THE GENUS LOLIUM.

L. perenne L.

Fertility. — In general the seed setting on isolation is very low, the average of isolations made in 1928 was 7,3 %. There are great differences between different plants, however, the individual values ranging between 0 and 34,7 %. The inter-plant variation is significantly greater than the intra-plant variation.

The seed setting on isolation is different in different years, but there is a marked positive correlation, $r = + 0{,}72$, between the seed setting of the same individuals in different years.

Inbred progenies after different mother-plants have significantly different percentages of seed setting on isolation, the averages for such progenies ranging between 0,1 and 26,9 seeds per panicle. There is a strong positive correlation, $r = + 0{,}91$, between the seed setting of the mother plant and the average seed setting of the inbred progeny. The heritable nature of the variation in isolation-fertility may, therefore, be considered clearly evident.

Besides the significant differences between the progeny averages, there is a wide variation between different plants in the same family, as regards isolation-fertility.

The seed setting in openly pollinated flowers was rather low in 1928, ranging between 3,5 % and 75,4 % in individual plants, with an average of 34,2 %. No correlation could be demonstrated between the seed setting on free flowering and that on isolation.

In most of the plants investigated the pollen was normally developed. In 5 plants, however, the percentage of normal pollen was low, and these plants must be considered as partially male sterile. No significant correlation could be demonstrated between pollen development and isolation-fertility. Between pollen development and general fertility of openly pollinated flowers there is a suggestive positive correlation, which indicates the existence of a close connection between male and female fertility.

Significant differences have been shown to exist between the different plants as regards size of panicle.

Inbreeding effects. — Chlorophyll-deficient seedlings rather often occur in inbred progenies, no definite factorial analysis could be made, however.

In the progenies of two different plants a dwarf-type was observed, which was completely sterile but developed bulbils at the nodes of the straws. Probably this dwarf is a double recessive.

The occurrence of other lethal factors is indicated by the low germination percentage in some families, which also gave some weak and abnormally developed seedlings.

Great variation in the inbred progenies was observed also in other characters, such as height, tillering, and leafiness, although no definite measurements were made.

On an average the isolation-fertility was lower in the inbred progeny than in the mother plant, the decrease being caused by the occurrence of plants with low vitality, which lower the average fertility.

L. multiflorum LAM.

Fertility. — The fertility upon isolation is very low, varying between 0 and 5,4 % in the plants investigated. No significant differences between the plants could be demonstrated, nor any such differences between the averages of different inbred progenies.

Between the isolation-fertility of the mother plant, and the average isolation-fertility of its inbred progeny there is a correlation of + 0,43. With the small number of pairs available, this correlation is not significant, and the heritable nature of isolation-fertility in *Lolium multiflorum* could, therefore, not be definitely proved.

From the investigations made on *L. perenne* and *L. multiflorum* it appears that the isolation-fertility is significantly lower in the latter species. If the inbred material of the two species is compared, the relation is the reverse. The cause of this reversion is twofold, viz. partly the occurrence of less vital plants in *L. perenne*, partly the fact that by chance the inbred family of this species having the largest number of individuals also shows the lowest degree of isolation-fertility.

The size of the panicles, as measured by the number of florets, is significantly different in different plants. A significant difference also exists between the two species, *L. multiflorum* having the largest number of florets per panicle.

Inbreeding effects. — Chlorophyll-deficient seedlings have been noted in the inbred progenies of 6 mother plants, but no factorial analysis was possible.

A large number of dead seeds occurred after isolation of 5 I_1 plants, all derived from the same mother plant. In the progenies of these I_1 plants abnormal seedlings and weak individuals were also rather common, all of which indicates a segregation in lethal factors.

The effect of inbreeding is in general less pronounced in *L. multiflorum* than in *L. perenne*, and unfavourable effects have been noted in fewer cases in the former species.

No average decrease in isolation-fertility from mother plant to inbred progeny could be demonstrated.

L. remotum SCHRANK *and L. temulentum* L.

A few plants of each of these species were isolated in 1930. The isolation-fertility was generally very high, in one plant of *L. remotum* even as high as 97,7 %, which indicates complete self-fertility.

b) THE GENUS FESTUCA.

F. rubra L.

Fertility. — The isolation-fertility of plants isolated in 1928 amounts to 3,8 % on an average, in 1929 the same value is 9,2 %. The variation between different plants is considerable, the extreme values in 1928 being 0 and 12,6 %, in 1929 0 and 41,5 %. In 1928 6 plants did not give any seed at all, in 1929 2 plants were equally sterile. Three of the sterile plants in 1928 were again isolated in 1929. Two plants were again completely sterile, the third one gave a very small amount of seed.

The seed setting on isolation differs significantly more between different bags on the same plant than between different panicles within the same bag. The variation between the plants is significantly larger than within the plants, which indicates hereditary differences between different plants as regards isolation-fertility.

The seed setting in openly pollinated flowers was only determined in 1928. The average value was 47,6 %, the individual plants ranging from 2,1 % to 85,6 %.

The isolation-fertility and the general fertility are significantly correlated, $r = + 0{,}49$. If that part of the isolation-fertility, which is correlated with general fertility, is eliminated there still remains a variation between the plants which is significantly larger than the variation within the plants. The existence of hereditary differences in isolation-fertility, independent of general fertility, is thus rather probable.

There are great differences between the different plants as regards size of panicle, measured by the number of florets.

Inbreeding effects. — A few albino plants were observed in one inbred family. The development of inbred and non-inbred progenies was observed, but no measurements were taken. The variability was greater in the *I* progenies than in the *K* progenies. In some cases, the vitality was apparently lower after selfing, in other cases no such effect of inbreeding could be observed.

F. ovina L.

Three plants of this species were isolated in a greenhouse in 1928. One of these plants did not give any seed at all, the two other gave 12 and 27 seeds on 30 and 73 panicles respectively.

c) THE GENUS POA.

P. pratensis L.

Fertility. — In 1929 52 plants of smooth-stalked meadow grass, belonging to different morphological types, were isolated. 5 of these plants were completely »self-sterile», 14 plants had less than 10 % seed setting while the others were fairly fertile, the maximum fertility being 78,9 % in one plant. The 5 »self-sterile» plants were again isolated in 1930. In this year, three of them were completely sterile upon isolation, a fourth plant gave 0,07 % seed, while one gave 21 % seed in 1930.

The seed setting in openly pollinated flowers was determined on 13 of the isolated plants. Different values were obtained, ranging from 2,6 % to 78,1 %, the average value being 55,1 %, whereas the average value of the same plants after isolation was 20,7 %. The variation in seed setting between the plants is insignificantly greater on free flowering than on isolation.

There is a positive correlation, $r = + 0{,}45$ (probability 90 : 10), between isolation-fertility and general fertility.

Inbreeding effects. — According to the observations made on inbred material, no unfavourable effect of the inbreeding seems to occur. Neither chlorophyll-deficient seedlings nor any other lethal or sublethal combinations were found.

d) THE GENUS ALOPECURUS.

A. pratensis L.

Fertility. — The isolation-fertility was determined on 16 plants in 1928, which gave an average of 3,4 seeds to the panicle cm. This value corresponds to about 9 % of the number of florets in a normal panicle. One of the plants was completely sterile upon isolation, the others gave values varying between 0,3 and 27,6 seeds to the panicle cm. corresponding to about 0,7 % and 73 % respectively of the number of florets.

The variation in seed setting between different bags on the same plant is not greater than the variation between panicles within the same bag. The inter-plant variation is significantly greater than the intra-plant variation, which indicates genotypical differences between the plants in isolation-fertility.

Even the panicle length is different in different plants.

The general fertility on open flowering has not been determined, nor have any studies been made concerning the effect of inbreeding.

IV. DISCUSSION.

1. FERTILITY AND STERILITY.

While the term fertility is used to denote the ability of sexual reproduction, the term sterility is used for such phenomena as impair this ability. Several authors have made attempts at a classification of the different causes of sterility. OELKERS (1927) has clearly defined lethality and sterility, and also distinguishes between sterility in the haplo-phase and the diplo-phase. CRANE and LAWRENCE (1929) distinguish between three kinds of sterility, viz. 1) generational sterility, 2) morphological sterility and 3) incompatibility. BRIEGER (1930) uses the terms »genuine sterility» (echte Sterilität) and »parasterility», the latter term is synonymous with incompatibility (STOUT 1917). MÜNTZING (1930) divides the sterility phenomena into two main classes, 1) sterility in a strict sense and 2) self-sterility and sterility due to modifying influences, and further he divides the sterility *sens. strict.* into haplontic and diplontic sterility.

In the author's grass investigations, part of which are recorded here, several kinds of sterility have been met with. Utilizing some of the above quoted distinctions and definitions, the following classification of the phenomena encountered has been adopted: 1) genuine sterility (haplontic or diplontic), caused by partial or absolute lethality in the haplo-phase or in the diplo-phase (MÜNTZING 1930); 2) modificative sterility, caused by environmental influences and 3) incompatibility, viz. the prevention of fertilization by genetic factors in spite of full vitality in the haplo-phase as well as in the diplo-phase. Incompatibility may prevent fertilization within an individual (self-incompatibility, self-sterility) or between different individuals (cross-incompatibility). The more complicated cases of non-fertilization between different species are also regarded as incompatibility.

In the investigations recorded here two kinds of fertility have

been studied, viz. general fertility, determined by the amount of seed setting on open flowering, and self-fertility, or rather isolation-fertility, measured by the amount of seed developed within isolation bags. General fertility and isolation-fertility were studied as separate characters, but attempts have also been made to determine to what extent isolation-fertility is dependent on different degrees of general fertility.

The analysis of variance has been extensively used as a means of distinguishing different causes for the variation in fertility. The variation between different panicles on the same plant (intra-plant variance) is caused entirely by modificatory influences by the environment, and thus offers a possibility of estimating quantitatively the effect of the environment. The variation between different plants (inter-plant variance) is caused, partly by environmental modifications, partly by genotypical differences between the plants. The environment must be assumed to cause a wider variation between different plants than between panicles of the same plant, but the inter-plant modifications are most probably of the same size-order as the intra-plant modifications, at least when no great differences in flowering time are involved. Thus, when the inter-plant variance is very much greater than the intra-plant variance, this may be taken as a strong indication of genotypical differentiation in the material.

The heritable nature of differences in fertility is also proved by correlations between the fertility-values of the same plants in different years. Such correlations may, to some extent, be caused by environmental influences, when the site of the plant is the same in both years. Transplantation must, however, set aside all environmental correlation, and therefore a correlation between the fertility-values of transplanted individuals in different years makes it possible to estimate a minimum value of the relative importance of constitutional differences. The influence of these genetical differences, however, may often be greater than that indicated by the correlation. The genetic constitution of an individual gives the *mode of reaction*. The different weather conditions in two years may easily reverse the relation between two different biotypes. All such reversals tend to diminish the correlations between different years, and may in extreme cases result in the total absence of any correlation, in spite of the fact that great genotypical differences exist.

General fertility. — For openly pollinated plants there is a theoretical possibility that 100 % of the florets in hermaphroditic individuals should give rise to viable seeds. In no instance in this in-

vestigation, however, has this value been attained, and a seed setting of 100 % seems to be very rare in allogamous gramineæ. (Cp. BEDDOWS 1931, TROLL 1931). Similar results have been obtained by HERIBERT NILSSON (1916) and ULRICH (1902) in rye. Even in autogamous species the 100 % point seems to be reached but very rarely (BEDDOWS 1931).

Even when no genuine sterility and no incompatibility impair the fructification, it may still be influenced to a considerable extent by environment. Discussions of this »modificatory sterility» can be found in papers by ERNST (1918) and TISCHLER (1928). For wind-pollinated grasses the weather conditions are probably of prevailing importance. It is a well-known fact in commercial seed-growing that different years are more or less favourable for pollination (SYLVÉN 1929). KNOLL (1929) has studied the influence of different environmental factors upon the seed setting and has shown that in many cases the absolute amount of moisture in the air is of fundamental importance, a negative correlation existing between seed setting and the absolute moisture-content of the air. FRUWIRTH (1916) has shown that light and temperature conditions have a great influence on the development of the sexual organs. No direct studies of the influence of different years upon the seed setting were made in this investigation and no data for general fertility in different years of the same material are available.

Genuine haplontic sterility, caused by partial lethality in the haplophase has been observed in a few cases. The cases of poorly developed pollen in *Lolium perenne* (p. 119) and *Poa pratensis* (F. NILSSON 1933 a) belong to this type of sterility. Positive correlation exists between the percentage of normal pollen and the degree of seed setting, and thus it seems probable that lethality in the male gametes is accompanied by a corresponding lethality in the female gametes, whereby the general fertility is decreased.

Genuine diplontic sterility has been observed in several cases. Those belonging to this group of phenomena are the lethal embryos in *Lolium perenne* (page 119), *L. multiflorum* (page 120) and *Phleum pratense* (page 94), chlorophyll-deficient seedlings and other weak individuals that never reach the stage of fructification. Other such cases are listed here as abnormal plants without functionating sexual organs, *e. g.* dwarfs in *Lolium perenne* (page 119), and individuals without any fertile straws or with abnormal spikes in *Dactylis* and *Phleum*.

A few interesting cases have been observed, where complete

diplontic sexual sterility was combined with the development of special organs for vegetative propagation. Sterile dwarfs of *Lolium perenne* were observed, which at the nodes had bulbils, capable of further development. Some *Dactylis*-plants with low fertility have a marked tendency to develop the florets into structures, very similar to the bulbils of true viviparous forms. No direct evidence was obtained that these »bulbils» develop rootlets, but it is very probable that under favourable conditions they may do so. Modificatory vivipary in grasses has been observed by JENKIN (1922), TINCKER (1925), THOENES (1929), TURESSON (1926, 1930 a) and BEDDOWS (1931). The last-mentioned writer has observed »plant-like structures» in sterile spikelets in *Cynosurus cristatus*, indicating the possibility for vegetative propagation, and writes: »These viviparous spikelets are rarely loosened, but the flower-heads may be so heavy that they lie upon the ground, in which position they are able to develop roots». The viviparous spikes of *Festuca ovina* behave in the very same manner (TURESSON 1926). The *nodosum* variety of timothy grass has often a very low fertility (compare pages 50 and 110 and also SYLVÉN 1929 and JENKIN 1931 d), but has in its stolons a means of vegetative propagation. Several cases are thus recorded among the grasses, in which sterility is associated with special organs for vegetative propagation.

Individuals with apparently normal spikes but without any seed setting have been observed in most of the species studied. As no close investigations were made, it is impossible to decide whether haplontic or diplontic sterility is present. In timothy purely male or female plants may occur. SYLVÉN (1929) has found cases of complete male sterility and WITTE (1919 b) has shown that this species is sometimes trioecious with male, female and hermaphroditic florets on different individuals. Even in other species a differentiation of the plants as regards sex may occur (compare JENKIN 1931 d, BEDDOWS 1931).

The possible occurrence of incompatibility could not be demonstrated in the material, but it does not seem impossible that in some cases it may have contributed to a decrease in the seed setting on open flowering. JENKIN (1931 d) has demonstrated »inter-sterility» in timothy, and has pointed out that the sterility of *nodosum*-plants, found by SYLVÉN (l. c.), might be caused by the lack of compatible pollen. In the material of the present investigation there is special reason to suspect incompatibility as a cause of decreased seed setting in inbred material. The inbred plants are mainly pollinated from their neighbouring sibs, and many of these may belong to the same biotype

as regards sterility factors. Under certain local or weather conditions the pollen from unrelated individuals may be insufficient, and incompatibility in combination with environmental factors may, therefore, in many cases considerably impair the seed setting.

In the species investigated there are very great differences between different plants in respect to seed setting in free flowering. The analysis of variance shows that these differences can hardly be due to environmental modifications only, but must be due to constitutional differences, causing genuine haplontic or diplontic sterility or even incompatibility.

Self-fertility. — Self-fertility is the capacity of the pollen to fertilize the eggs of the same plant. In older days only pollination within the same flower was counted as self-fertilization (HILDEBRAND 1872, GODRON 1873). DARWIN (1876) gave the modern definition, which is correct from a genetical point of view, *i. e.* self-pollination means pollination within the same individual, cross-pollination takes place, when the eggs are pollinated with pollen »from a distinct plant of the same species».

The first to demonstrate self-sterility was KÖLREUTER (1764) in *Verbascum phoeniceum.* His results were corroborated by DARWIN (1876) who made extensive studies of self- and cross-pollination in different plants. At present there is an immense literature on the subject of self-fertility in a great number of plant species (for reference see LEHMANN 1928, EAST 1929, BRIEGER 1930). The thorough investigations made, especially in *Nicotiana*, have resulted in a genetical theory of self-sterility, which explains a majority of the phenomena observed. According to this theory, self-sterility factors in series of multiple allelomorphs are the cause of the grouping of the individuals into intra-sterile but inter-fertile groups.

The first attempts to determine the seed setting on isolation in gramineæ were made by WILSON (1876) in barley, RIMPAU (1877) in rye and KÖRNICKE (1890) in herbage grasses. Since then numerous investigations have been made, among which may be especially mentioned those by FRUWIRTH (1916), FRANDSEN (1917), CLARKE (1927), KNOLL (1929), GREGOR (1928), SYLVÉN (1929), JENKIN (1931 a), TROLL (1931), BEDDOWS (1931) and VALLE (1931 a and b). A complete list of the literature is given by BEDDOWS (1931).

It is very difficult to determine the exact degree of self-fertility, since all the different methods for the exclusion of foreign pollen involve factors that may influence the degree of seed setting more or

less. Isolation by distance offers the most natural conditions for the development of seed, but by this method foreign pollen cannot be excluded with absolute certainty. In most cases, therefore, different devices have been used, in which plants or inflorescences have been enclosed. KNOLL (1929) has shown that more natural conditions for development are obtained by enclosing only the panicles and not the whole plants. SYLVÉN (1929) has studied the influence upon the seed setting of the number of panicles enclosed in one bag and of the mode of attaching the bag to the supporter. From the results he concludes that the best seed setting is obtained when several panicles are enclosed in each bag, and the bags are not fixed to any kind of support.

On the other hand, KNOLL (l. c.) maintains that if many panicles are enclosed in the same bag, the ensuing increase in moisture will be unfavourable for pollination.

Pergamine bags are becoming more and more used as isolating material, and seem to give good results. One drawback of these bags is, however, that they are easily damaged by wind and rain, and that therefore a considerable number of isolations must be discarded. That the pergamine bags, used in the investigations recorded here, have not had any detrimental influence upon the seed is indicated among other things by the fact that the germination percentage, investigated in one group of material, was even higher in the isolated than in the non-isolated seed (page 94). That unfavourable conditions inside the bags are of comparatively small importance for the output of seed is shown by the wide variation in seed setting between different isolated individuals, and especially by the fact that in self-fertile species (page 121 and unpublished data) an almost complete seed setting is obtained within the bags.

By enclosing the panicles pollination may be more or less prevented. Investigations by SYLVÉN (l. c.) on timothy and cocksfoot have shown, however, that in these grasses the pollination within the bags is fairly good, and on an average artificial selfing within the bags did not increase the seed setting. If the bags are large enough and not too firmly attached to the supporter, a deficiency in pollination will hardly cause any considerable decrease in the seed setting.

Thus, if it can be maintained that modificatory influences by the isolation bags cannot be the main cause of low seed setting on isolation, it is nevertheless probable that the real self-fertility is higher than the results obtained indicate. If by self-fertility we mean the maximum seed setting to be obtained under extremely favourable conditions, then

the average value of several isolated panicles on each plant will nearly always be too low. Even if neither genuine sterility nor incompatibility are present, and even if the bags as such do not exercise any unfavourable influences, the seed setting will be impaired by modificatory influences in many cases, just as is the case in open pollination (compare FRUWIRTH 1916, 1917, KNOLL 1929). SYLVÉN (1929) uses the highest values, obtained from single panicles, as a measure of the self-fertility. These values will, no doubt, approach the maximum self-fertility more than the averages, but they give no exact information as to what may be accomplished under the most favourable conditions. If we wish to study the variation in self-fertility between different individuals and different populations, the averages are better than the maximum within each plant. Using only the highest single panicle value of each plant, we must calculate with very great modificatory differences between plants, and we lose all possibilities of judging quantitatively the influence of modifications. If the average of several panicles from each plant is used, the modificatory differences between plants are greatly reduced, and the variation between panicles on the same plant offers a means of estimating the importance of modifications. We have only to keep in mind that the self-fertility values, used in this investigation, are not absolute values, but relative, offering the best measure available of the *different degrees of self-fertility*, encountered in different individuals and populations.

As has been stated, modifications of different kinds may impair the seed setting within the bags. The importance of the modifications is measured by the differences between different isolated panicles on the same plant as regards seed setting. The cause of modifications may be of different kinds. Some of them have been mentioned in discussing the method of isolating employed, but is has been shown that the abnormal conditions within the bags must be of comparatively little importance. That the bagging has some influence is shown by the fact that in some groups of material the variation is greater between isolated panicles than between free (page 47). Indirectly the isolation may increase the modifications, since the bagging may exaggerate the influence of weather conditions at the time of pollination. Very important causes of modifications are accidental injuries, which are more likely to hurt the isolated panicles than the free ones. Among such accidental injuries may be mentioned parasites and mechanical damages. Parasites, fungi and insects, have not been observed to harm the isolated panicles but it has not been possible entirely to avoid me-

chanical injuries. Great damage has been observed, causing the material to be discarded, but even invisible breaks in the straw may prevent the circulation and cause sterility. Minor mechanical injuries are probably the cause of sterility in some panicles, when other panicles of the same plant give much seed (page 43).

Besides the factors mentioned, which may cause differences between panicles on the same plant, and also between different plants, there are others, which may cause further differences between different plants or between plantlets belonging to the same clone. Such factors are modifications in the vigour of the plant, the amount of moisture and nutrient in the soil etc. JENKIN (1931 b) has found very great differences between different results from one and the same individual in *Lolium perenne*, and writes: ». . . it may be noted that the variation in the results for any particular plant appears not to be due to any single and obvious environmental factor, although it has been suggested that the vigour of the plant or plantlet may to some extent be correlated with degree of self-fertility shown in the results. Such correlation is, however, by no means constant and absolute, so that it cannot account except to a very slight extent for the extreme range of fluctuation shown by each of these plants. These results, therefore, may be considered to represent approximately what is generally to be expected, and they show that a single result or even a few results cannot be regarded as anything but an approximate representation of the potential self-fertility of the plant concerned».

The causes of modifications, which do not express themselves in differences between panicles on the same plant, but only in differences between plants, cannot be quantitatively estimated by the intra-plant variation. In one case, however, (pages 59 and 92) the material has been clonally propagated, and the variation between plantlets of the same clone furnishes an estimate of the modifying influences, operative only between plants. The variation between the plantlets is greater than that within the plantlets, thus supplying full evidence for the existence of modificatory influences, manifesting themselves only in plant-differences.

Besides the differences in seed setting on isolation, caused by the various environmental factors, now under discussion, there are also genetical differences in this respect, as has been pointed out by several authors (WITTE 1919 a, SYLVÉN 1929, KNOLL 1929, VALLE 1931 b, JENKIN 1931 b and c, GREGOR 1928 and others). The existence of genetical differences between plants may be proved in different ways.

If there is a correlation between the degrees of seed setting in the same individuals under different environmental conditions, this proves the existence of genetical differentiation between individuals. The limitations of this method have been discussed already (page 124). HAYES and BARKER (1922) and HAYES and CLARKE (1925) have found such correlations in timothy grass, and even in the present investigation such correlations have been demonstrated (page 50).

Another way of proving the existence of genetical differences is to demonstrate that the differences between plants is too great to have been caused by the modifications. In most groups of material the variation between plants is very much greater than that within plants, which should prove the existence of genetical differences. It was mentioned above, however, that the plant-differences are to some extent caused by further environmental influences, not measured by the intra-plant variation. The clonal material, however, offers a means of estimating the size of the inter-plant modifications, and these are decidedly smaller than the total inter-plant variation. In one family, where all individuals have formed clones, the inter-clone variation is directly comparable with the inter-plantlet variation within the clones, and here definite proof could be advanced that the individuals were genotypically different. But even in the other groups of material the inter-plant variation is so much greater than the inter-plantlet variation in the case mentioned that it may be considered quite certain that genotypical differences exist between the plants. In a few cases the material is too scanty for any definite statement, and in *Lolium multiflorum* the differences between plants are so small that they might have been caused entirely by environmental influences, in this species, therefore, no genetical differentiation could be demonstrated. In the highly self-fertile species *Lolium remotum* and *L. temulentum* it is possible that all individuals are quite self-fertile, and that no genetical differentiation in this respect occurs.

The heritable nature of differential self-fertility is further proved by the correlation between mother plant and progeny in this respect. Such correlations could be shown to exist in *Lolium perenne* and *Phleum pratense*.

The factorial basis of self-fertility could not be ascertained, but a very wide segregation was observed after different isolated mother plants in *Lolium perenne* and *Phleum pratense*. The degree of differentiation is, however, very different in different progenies, probably depending upon different genotypical constitutions of the mother

plants. In some inbred families of timothy all plants have a comparatively high degree of self-fertility, in other families all individuals are nearly or completely self-sterile, most families again show a wide segregation. Selection for high degrees of self-fertility has, therefore, in many cases good results [compare HERIBERT NILSSON's (1916) results in rye]. In no instance has a family shown an apparently constant intermediate degree of self-fertility. This indicates that only a few factors, having a great effect, are mainly responsible for the genetical variation in this character, while modifiers must be supposed to cause smaller gradations. The material does not permit of any definite statements to this effect, but the results agree completely with those obtained by VALLE (1931 b).

The low degree of self-fertility, found in most instances, is probably due chiefly to self-incompatibility, but also genuine sterility may occur. In the cases where haplontic or diplontic genuine sterility impairs the general fertility, the low degree of self-fertility must be ascribed to the same causes. Haplontic sterility seems to be the cause of the »self-sterility» in three cases in *Poa pratensis*. A partial haplontic sterility in the male gametes occurring in *Lolium perenne* has apparently had no influence on the self-fertility, since no correlation exists between the percentage of normal pollen and the percentage of seed setting on isolation. The probable explanation is that the self-fertility is so low that even a considerable male sterility does not appreciably influence it: there is always enough viable pollen to accomplish the few self-fertilizations possible. Further, modifications may disguise a weak existent correlation.

Different morphological types of timothy have different average degrees of self-fertility. In the investigations recorded here, the *nodosum*-variety was decidedly less self-fertile than the tall hay-type. Similar results were obtained by SYLVÉN (1929) and JENKIN (1931 d). The difference is very great, and may depend on differences in chromosome number, which is 14 in *nodosum* and 42 in the erect type (GREGOR and SANSOME 1930). As pointed out by LAWRENCE (1930) and MÜNTZING (1932 a) polyploid species are in general more self-fertile than diploids, which may have to do with different numbers of sterility or fertility genes.

Different strains of tall timothy also have different average degrees of self-fertility. The *Kämpe* strain, derived from *Finnish* timothy, is on an average much less self-fertile than strain *121*, derived from Swedish stock. Here is an indication, as in TROLL's (1931) investiga-

tions, that timothy grass from different regions may show different degrees of self-fertility, which might explain the contradictory results obtained by investigators in different countries.

The opinion has often been expressed that inbreeding causes a decrease in fertility. The results presented here do not support the theory that inbreeding, as such, causes a general lowering of the fertility, but they indicate a segregation into widely different types, fertile as well as sterile. As already mentioned, there is a very marked differentiation as regards self-fertility between individual plants of inbred progenies, and further, sterile segregates appear. These may have diplontic or haplontic sterility, and in the latter case the sterility may occur in both sexes or only in one of them. In extreme cases this may result in a differentiation into monoecious, dioecious and trioecious strains (see page 126). A sex-differentiation has also been observed by JONES (1918) to occur in maize, he writes: ». . . inbreeding is bringing about a tendency for maize to change from a functionally monoecious plant to a functionally dioecious plant, although, morphologically, both staminate and pistillate parts are present». (Also compare JONES 1931.) The segregation of sterile types has also been observed in *Drosophila* (MOENKHAUS 1911, HYDE 1924) and by WRIGHT (1922 a and b) in guinea pigs, where also different types of sterility could be distinguished.

Some I_3 plants of strain *121* give very high seed setting on isolation, while others are completely self-sterile. This again proves that inbreeding has no general effect on self-fertility, but simply brings about a differentiation into different biotypes.

CLARKE (1927) found a correlation between vigour and fertility. In the present investigation such correlations are also found. Plants with rather low vitality are generally unable to develop much seed, and in timothy grass correlations have been determined between height and fertility (page 90). Other quantitative characters may also be correlated with fertility, but in the more closely investigated cases these characters are then correlated with the height, in the same manner as the fertility, and if the common correlation with the height is eliminated, by calculating partial correlations, then no independent correlation is found between fertility and other characters. In some cases at least where fertility is correlated with height there are, however, strong indications of a variation in fertility, which is independent of the height.

Correlations between general fertility and self-fertility. — Correla-

tions between general fertility and isolation-fertility could be demonstrated in *Festuca rubra*, *F. pratensis*, *Poa pratensis* and *Phleum pratense*, but not in *Lolium perenne* or *L. multiflorum*. The correlations need not, however, necessarily indicate a deep connection between general fertility and self-fertility. Parallel modifications may influence the seed setting inside as well as outside the bags, resulting in a correlation. In extreme cases, however, common genetical causes for general and self-fertility must be assumed. The fact that segregates with diplontic or haplontic sterility are also more or less self-sterile has just been mentioned, and the present material offers several instances of this parallelism between general and self-sterility.

One other fact may cause a correlation between general fertility and self-fertility, viz. the fact that in inbred material the individuals are surrounded by plants belonging to the same family. Most of the pollen available probably comes from the neighbours in the field, and since these are closely related there are great possibilities of their belonging to the same intra-sterile group as the selected mother plant of the family. This fact may, as already mentioned, possibly influence the seed setting in general, and also bring about a correlation between apparent general fertility and self-fertility.

There is, thus, a correlation between general and self-fertility, inasmuch as, in many cases, decreases in both kinds of fertility are due to common causes. By the aid of an analysis of variance it is, however, possible to show, with great probability, that there is also a variation in self-fertility, independent of the general fertility. By means of the regression of self-fertility upon general fertility it is then possible to deduct that part of the variation in the former which is parallel to variation in the latter. The remaining variation in self-fertility between plants is greater than the variation within plants, and it is also much greater than the modificatory variation between plantlets, found in clonal material (compare page 89). This remaining variation is, therefore, most probably not caused only by environmental influences but is of a genotypical nature. It has, thus, been possible to distinguish between fertility in general and self-fertility, and to show that even in a material, homogeneous in regard to general fertility, there will occur differences in self-fertility, and that this latter is an independent character.

These studies of fertility have as their main result furnished evidence that a wide differentiation is found in nature, between indi-

viduals and also between different commercial strains, products of previous breeding work or different populations of cultivated grasses. They have, further, shown that the self-fertility is to a great extent dependent upon the degree of general fertility, and to some extent also upon the general vigour of the plants, as measured by the height or other quantitative characters. They also point to the great probability of the existence of a genetic variation in self-fertility, independent of general fertility and vigour. Finally, as far as the effect of inbreeding upon self-fertility is concerned, the material investigated has presented no general decrease in self-fertility as the result of inbreeding. Inbreeding brings about a differentiation, in general vigour as in general fertility, and also with respect to the special factors for self-sterility. Several plants must, therefore, occur with very greatly impaired self-fertility, but at the same time highly self-fertile individuals are obtained even after several generations of inbreeding.

2. INBREEDING EFFECTS.

Brief review of the theories of inbreeding. — It is an old commonplace in biology that hybridization brings about increased vigour, »hybrid vigour», and that »deleterious effects» of inbreeding are often encountered. It was very difficult, however, to give a satisfactory explanation of these phenomena, and indeed no such explanations were possible until orderly experiments were carried out and our knowledge of heredity had been deepened by the rediscovery of the Mendelian laws. A review of all modern literature upon the subject would require a book, therefore only the most important points shall be mentioned, and for details the reader is referred to the comprehensive papers by EAST and HAYES (1912), JONES (1918), EAST and JONES (1919), FEDERLEY (1928) and SIRKS (1929). Among pre-mendelian studies those of KÖLREUTER (1766) are of interest, since they represent the first instance of systematic studies of artificial hybrids, and since they offer several striking instances of hybrid vigour. The most important studies during this period are the extensive investigations of DARWIN (1876), who made several observations which have later been repeated and given their Mendelian explanation. DARWIN found that the deleterious effects of inbreeding did not continue in more closely inbred plants, but that they were less considerable in the 7th, 8th and 9th generations than in the 1st, 2nd and 3rd. In later generations great uniformity in colour was obtained. It made no difference, whether the individuals in an inbred lot were selfed or intercrossed, which DARWIN explains by the

assumption that these individuals were »germinally alike». Crossing a closely inbred strain with a less inbred one did not give so great an increase in vigour, as if a »fresh stock» was used. DARWIN was also the first to give an explanation of hybrid vigour, and he did not ascribe the effect to the crossing as such but to the combination of diverse sexual elements. Also in autogamous species hybrid vigour was obtained by crossing entirely different strains. MENDEL (1865) also observed hybrid vigour in his pea crosses, . . . »a fact which is possibly only attributable to the greater luxuriance which appears in all parts of plants when stems of very different lengths are crossed» (quoted from JONES 1918).

In the present century hybrid vigour and inbreeding degeneration have been closely studied from the view-points given by MENDEL's laws, JOHANNSEN's genotype-conception, NILSSON-EHLE's multiple factors and the explanation of linkage given by MORGAN and his co-workers. Intensive studies on a large scale have been carried out in several allogamous species, in order to explain the effects of inbreeding and the occurrence of hybrid vigour. Especially, the investigations in maize by the American scientists EAST and HAYES (1912), SHULL (1910) and JONES (1917, 1918, 1924) have thrown light on what happens during inbreeding for several successive generations. These results were made the foundation of the theory of »heterosis» (SHULL 1911, EAST and HAYES 1912), which explains the decrease in vigour after inbreeding as the immediate result of the increase in homozygosity that must follow. The »heterosis» theory assumed that heterozygosity as such has a stimulating effect upon cell-divisions and growth and thereby upon general vigour. The theory could not, however, explain all observed phenomena, *e. g.* the varying effect of inbreeding or the fact that crossing sometimes does not bring about an increase in vigour but the opposite. SHULL had already observed this, and states that sometimes heterosis may be without effect, or even have an unfavourable one. Further examples of cross-depression have been given from autogamous species (ROSENQUIST 1931) and recently by NILSSON-LEISSNER (1933) and the present investigation (*e. g.* Tables 57 and 58).

The Mendelian explanation of hybrid vigour, generally called the »dominance-theory» was first founded on results gained in autogamous plants. KEEBLE and PELLEW (1910) found luxuriance in F_1 of a cross between different varieties of peas, and ascribed it to dominance of different factors, brought together by the cross. BRUCE (1910) also suggested that dominance might cause hybrid vigour, since most factors

are dominant, and the heterozygosity is highest in cross-products. JONES (1917, 1918) further developed the dominance-theory, and especially tried to explain the symmetrical distribution in F_2 and the difficulty to obtain the parental types in this generation by the assumption of a linkage between a great number of growth-factors. EAST and HAYES (1912) objected to the dominance theory, pointing out that according to this theory inbreeding effect does not always occur, and that vigorous types should be obtained in addition to the degenerated ones. EMERSON and EAST (1913) studied quantitative characters, and mentioned symmetrical distributions in F_2 whereas dominance should have brought about negative skewness. COLLINS (1921) made the remark that, if a great number of factors are at work, the skewness will be very little apparent, unless a very great number of individuals is grown. He also demonstrates what small chances there are of obtaining F_2 individuals with full vigour, if many factors segregate, and he considers it unnecessary to involve linkage in the explanation of the inbreeding effect.

In the course of years the dominance theory has been more generally accepted, by EAST (EAST and JONES 1919) and HAYES (1926), and seems at present to have very few opponents. Even in animal genetics the dominance theory has been used, for instance, by KING (1918 a and b), WRIGHT (1922 a and b), and LIVESAY (1930). Hybrid vigour, obtained after crossing of autogamous plants has in several instances been possible of explanation by the dominance theory, *e. g.* in bean (MALINOWSKI 1928), oats (COFFMAN and WIEBE 1930), *Galeopsis* in species crosses (MÜNTZING 1930), wheat (ROSENQUIST 1931). The old opinion that cross-pollination, in contradistinction to self-pollination, stimulates the growth of the plants has been definitely disproved by experiments with pure lines (NILSSON-EHLE 1927).

Partial and general inbreeding depression. — In the discussion on different inbreeding-theories, two kinds of depression after inbreeding have been distinguished, viz. 1) partial depression, *i. e.* the occurrence of abnormal and inviable individuals, and 2) general depression, *i. e.* a general decrease in vigour, not directly referable to any special character, appearing in the inbred progeny as compared with the outbred. The partial depression was explained early on Mendelian basis as the result of a segregation in lethal or sub-lethal factors, and several examples of such segregations have been given, some of them monofactorial, others more complicated (see NILSSON-EHLE 1926, 1927). Among animals, abnormal individuals such as albinos, dwarfs etc. are rather common

(see WRIEDT 1925). In plants the most common types of degenerate recessives are the chlorophyll-deficient types, but also dwarfs and other abnormalities of different kinds occur. Several new cases of such abnormalities of different kinds have been encountered in the course of the present investigation.

The general depression was more difficult to explain on Mendelian basis, but since the laws of quantitative inheritance became known even this kind of depression was more easily understood. The fact that the development in each character depends on a large number of factors makes the genetical basis of these characters difficult to analyse, and the difficulties are further increased by the existence of »modifiers» that conceal the effect of eventual main factors. (See discussion by TEDIN 1925). The analysis becomes still more complicated if the cumulative effect of each factor is not specific but depends to a high degree on the constitution of the plant, as regards other factors having a similar effect, a point thoroughly discussed by RASMUSSON (1933) in his presentation of the »interaction-hypothesis».

The general inbreeding depression manifests itself by decreased vigour, and »vigour» must be considered to be still more complicated than single characters, such as height, and, therefore, still more impossible to analyse genetically. Studies of the inbreeding effect must be confined to studies of single characters of a more or less complicated nature. Such investigations of single characters have been carried out, among others, by JONES (1918, 1924) in maize and by WRIGHT (1922 a and b) on guinea pigs. Those investigations of separate characters have shown that there is no fundamental difference between partial depression and general depression. The »general» depression is not really general, but manifests itself now in one character now in another or several others (WRIGHT 1922, HERIBERT NILSSON 1926), which may be explained by the different genotypical constitutions of inbred mother individuals. The only difference existing between »partial» and »general» depression is the degree of complicate inheritance of the characters involved.

The determination of inbreeding effect. — Theoretically, the effect of inbreeding must be considered to be the difference between the selfed individual and its inbred progeny. Owing to sundry technical difficulties it is not always possible, however, to obtain the direct comparison between mother individual and progeny. The greatest difficulties are met with in dioecious plants and non-hermaphroditic animals, where selfing is impossible. Since none of the grasses studied

here are dioecious, such organisms are left out of the discussion, which is confined to hermaphroditic plants.

In annual plants it is impossible to compare mother plant and progeny. In such cases the inbred progeny is compared with cross-bred progeny or with the average of the population, *i. e.* the comparison is made between inbred and outbred progenies. The same method has also often been employed in perennial grasses, and the inbred progeny has been compared with cross-bred progeny of the same mother plant, either obtained by artificial pollination with a known male (JENKIN 1926) or by free pollination with unknown pollen-deliverers (WITTE 1919 a, KIRK 1927, TORSSELL 1930, VALLE 1931 a and b, NILSSON-LEISSNER 1933). In the investigations presented here the latter method has been applied in the majority of the cases, but in some instances the inbred progeny has been compared with a clone of the mother individual.

Assuming that no self-fertilization takes place, the comparison between inbred progeny and progeny after open pollination might be assumed to give the correct value for the difference between the inbred generation and a generation without inbreeding (I_0). This is not true, however, irrespective of the fact that self-fertilization always occurs in varying degrees, according to the results obtained in this investigation. The progeny after open pollination (K) is to a very great extent dependent on the constitution of the functionating male plants. Since most of the fertilizing pollen must be supposed to be derived from neighbouring plants, chance occurrences or planting technique may have a very great influence upon the constitution of the K family, and thus upon the measurement obtained of the effect of inbreeding. If the plants surrounding the mother individual represent minus variations as compared with the latter, the K family may be considerably lower than the mother individual, and thus the comparison between inbred material (I) and K may completely conceal any existing inbreeding effects. A striking case in *Festuca rubra* has been reported by NILSSON-LEISSNER (1933), who points out that even if the K progeny may be considered as free from inbreeding, it does not always give values suitable for a comparison with the I progeny so as to determine the effect of inbreeding. Another similar case may be added from the present material (page 99), where the K progeny of an I_2 plant was significantly lower than the mother plant, represented by clone-plantlets.

On the other hand, in many cases the open pollinated progeny, the K progeny, may show a luxuriation as compared with the mother

individual. Such a luxuriation in *K* becomes more probable, and also in the present material more common, the more closely inbred the mother plants are. Luxuriation may occur, however, even in *K* progenies of I_0 plants. In this investigation luxuriation after free pollination was observed in the progeny after some low plants of *Russian* timothy, belonging to the *nodosum*-type (Table 57) but they were surrounded by tall plants in the same population. This instance offers a striking parallel to the results of NILSSON-LEISSNER (l. c.), although the influence of the male plant is the opposite in this case.

That the luxuriation in *K* progenies becomes more marked with increased inbreeding of the mother plants is strongly suggested by the material, where both *K* and *I* could be compared with the mother clone (Tables on page 114). The material is too small to supply a definite proof, but one fact is certain, however, viz., that the difference between *K* and *I* progenies in this material is, on an average, greater than the difference between mother clone and *I* progeny. This proves that comparisons between *I* and *K* will cause an over-estimation of the effect of inbreeding, an over-estimation which will probably increase with increased inbreeding of the mother plant and which may, in extreme cases, lead to the result that the »inbreeding effect» increases at the inbreeding is continued.

If the plants of an inbred family are planted in blocks or in rows, so that each plant is surrounded by other nearly related plants, the luxuriation in *K* may be expected to be less pronounced. In this case *K* is also a product of inbreeding, even if not so close as selfing, and the comparison between *I* and *K* is not a comparison between I_n and I_o but between two families with different degrees of inbreeding, which degree cannot be accurately determined at least for one of the families.

Only if the selected mother plants represent about the average of the population and are surrounded by uniformly »average» plants within a not too heterogenous I_o population, the *K* progeny may be considered as a fair representative of the mother individual. In all other instances the comparison between *I* and *K* may lead to gross mis-interpretations of the results, especially if the difference is taken as a measure of the effect of inbreeding from one *I* generation to the following.

In view of the given analysis of the measures of inbreeding effect, which analysis is founded on current theories and on experimental data, we are justified in expressing very strong doubts concerning the conclusions drawn by VALLE (1931 b). Basing his statements on comparisons

between *I* and *K* progenies in different inbred generations he maintains that in timothy the effect of inbreeding increases in consecutive generations and that, therefore, on this species there cannot be a minimum value, at which inbreeding has no further effect.

In perennial plants it is possible to obtain an accurate measurement of the degree of inbreeding by a comparison between the inbred progeny and a clone of the mother plant. Even in this method, however, considerable difficulties are encountered. Cutting and transplanting are severe checks in the normal development of the plant and may have considerable effects, and, further, the individuals to be compared are not of the same age, a fact that may influence the modificability of the plants. In order to avoid these difficulties it might seem advisable to let the progeny individuals reach the age of two years, and then to make clones of mother individuals and progeny simultaneously. This method again offers technical difficulties and introduces a new source of error. Before the seedling progenies can be divided for clonal propagation they must have reached one or two years of age. During this time a number of the weaker plants will have succumbed, and the comparison between mother clone and progeny will again not present a true picture of what has really taken place. A compromising method has been employed in some cases in this investigation, in that the mother individuals have been divided, and cuttings of them, of about the same size as the seedlings, transplanted simultaneously with the transplantation of the latter into the experimental field.

In spite of the limited possibilities for drawing conclusions from comparisons between *I* and *K* progenies, such comparisons have a certain interest. This is especially the case, when the mother plants are strongly inbred and surrounded by plants from the same nearly homozygous family. In this case a comparison may be made between selfing and open pollination, with pollen of approximately the same genotypic constitution in both cases, and it might be possible to demonstrate any detrimental effect of selfing. No such influence could be demonstrated in this investigation, on the other hand, it was possible to show that in itself neither the isolation nor the selfing constitutes the main cause for the frequently observed decrease in vigour in inbred material. In some cases the *K* progeny was significantly lower than the *I* progeny and this shows, at any rate, that the factorial constitution of the progeny, dependent on the mother plant, and in *K* progenies also on the male plants, is much more important than the modifying influence of the isolating bags, or the eventual effect of the enforced inbreeding as such.

Designation of I_0 and I_n. — The literature on inbreeding deals very little with the problem as to when a material may be correctly denoted as I_0. The theoretical I_0 population ought to consist of individuals, heterozygous in all segregating factors present, and inbred generations after such individuals should be denoted as I_1, I_2 etc. Even in obligate allogamous species, however, such I_0 individuals are very rare, and we cannot expect the selected individuals to be totally heterozygous, they are all more or less homozygous, and therefore, from a theoretical point of view, they may be considered to represent different inbred generations within one and the same population. The different constitution of different plants leads to different results when they are isolated, and the degree of inbreeding effect as well as the characters in which it becomes apparent, are dependent on the genetical constitution of the mother plant. For this reason the number of heterozygous factors in this plant is of importance, and so is their qualitative and quantitative influence in the phenotypical development. The genetical constitution of the initial plant also determines the inbreeding minimum of the progeny. This inbreeding minimum may be different in different lines of descendants, but the minimum and maximum values for the final homozygous populations are given by the constitution of the initial plants.

The facts just stated may be considered as rather commonplace from the point of view of current theories of inbreeding. They are sometimes forgotten, however, and false conclusions accordingly drawn. The great variability in the results of inbreeding, expected according to the dominance theory, especially as unfolded first by JONES (1917) and then by RASMUSSON (1933), should urge the greatest care in generalizing results obtained from investigations made on a limited material. In this connection it may only be added that not only in populations of cultivated plants are different degrees of homozygosity to be expected, but the same holds true also for wild plants. Wild species are divided into numerous more or less isolated populations, each with a rather limited range of variation, the limitation being caused either by chance in the migration of plants or by natural selection, as shown especially by TURESSON (1922 and other papers).

Every existing plant population, except perhaps some F_1 generations of artificial hybrids, may be considered to have been the subject of some inbreeding, by nature or by man, consciously or unconsciously. And the degree of previous inbreeding is in most cases unknown, and may be ascertained only by exceedingly *extensive* investigations. It

may therefore easily occur that an »I_0» population, wild or in culture, is more homozygous, and thus *more inbred,* than an I_1 or I_2 population derived by artificial inbreeding of individuals from, in this respect, unknown initial populations. Under such conditions it is futile to distinguish sharply between material, previously inbred and I_0 material, unless the different groups of material can be put in direct relation to one and the same initial plant or isogenic population, used as the *origo* in determining the degree of inbreeding.

From the above it is clear that when some of the initial populations in this investigation are denoted as I_0, others as I_1, this is taken only to be a very approximate characterization of their degree of inbreeding, denoting the generations of *controlled* inbreeding in the pedigree of the populations.

Inbreeding effect or isolation effect. — In judging the effect of inbreeding the eventual modificatory effect of the isolating bags must always be taken into account. The abnormal conditions within the isolating bags may result in a poor development of the seed, and this again may cause a poor development of the seedlings, whereby the plants are set back during the whole of their life-time. On different occasions in the previous discussion it was pointed out (pages 128 and 130), that the results obtained in this investigation cannot be explained only by assuming a detrimental influence of the abnormal environment within the bags. A few more points concerning this question will be discussed, however.

In rye (HERIBERT NILSSON 1916, 1921) as well as in timothy (VALLE 1931 b) it has been shown that the weight of 1000 seeds as well as their germinating capacity are lower in isolated than in openly pollinated flowers. This does not seem, however, to be the case in all instances. VALLE writes that ». . . in zahlreichen Fällen, wo der Samenansatz nach Selbstung sehr gering war, der in Isolierung entwickelte Samen grösser wurde als bei denselben Pflanzen nach freiem Abblühen». Two opposite kinds of modifications may influence the seed development within isolating bags. The abnormal conditions within the bags are likely to weaken the seed, but on the other hand, the amount of nourishment, available for each seed, is very high in plants with low self-fertility, and this may counteract the unfavourable influence of the enclosure.

The influence of poor development of the seed upon the further growth of the plants is not sufficiently known. In annual plants it is a well-known fact that poorly developed seeds also give poor seedlings

and plants with a low productive capacity. In perennial plants, however, it may be supposed that differences in the seedling stage, caused by differences in the seed development, will gradually disappear as the plants grow older, and according to the author's experience it is very doubtful whether 2—3 year old plants show any influence of the seed-quality. At least this influence cannot possibly cause the great differences observed in this material.

The unfavourable effect of the enclosure might also cause a low percentage of germination in the isolated seed. The only comparison available in this material shows, however, an insignificantly higher percentage of germination after isolation than after free flowering. This does not indicate that any great influence is to be ascribed to the enclosure, and as will be shown in the following section, the influence of inbreeding upon the germinating power of the seed is most probably caused by segregation in lethal factors.

Effect of inbreeding on germination and winter hardiness. — From the results in *Lolium perenne*, *L. multiflorum* and *Phleum pratense* it is evident that the genotypical constitution of the mother plant is of great importance for the germination of the seed.

As stated above, isolated seed germinated better than non-isolated in comparisons made in timothy. There is a marked correlation between the germination of isolated and non-isolated seed from the same plant. This correlation might be caused by parallel modifications, but it is more probably due to genetical factors. This is also indicated by the fact, that in families with low germination there also occur numerous abnormal seedlings and other kinds of sub-lethal abnormalities. Inherited »line differences in the germination energy of the seeds» in *Galeopsis* have been found by MÜNTZING (1930). The differences in percentage of germination between different families, observed in the present investigations, seem to be due to lethal factors, active in the embryonic stage.

As regards winter hardiness in timothy a marked effect of inbreeding could be demonstrated. Inbred families have on an average a higher mortality than the corresponding *K* families, and there are greater differences between *I* families than between *K* families. The families, with a high rate of mortality also show several plants with more or less deficient chlorophyll development or with other abnormalities. Further, the rate of mortality is highest in those families which show the widest variation in morphological characters. It is, therefore, probable that the low degree of winter hardiness in some

cases is not due to the inbreeding as such, but depends on the segregation of individuals, homozygous in sub-lethal factors.

Inbreeding effects in height and some other characters. — In all the material great differences between progenies after different mother plants are apparent, and this differentiation is very marked in isolated progenies as well as those after open pollination. In some cases the differentiation is greater after isolation, in others no such differences could be demonstrated. Thus, the genotypical constitution of the mother plant is of very great importance for the progeny, quite independently of the male plants. This influence of the mother plant might be due to a certain degree of spontaneous selfing, but the generally low degree of selfing on isolation does not indicate that this factor is of any great importance. Pollination mainly by neighbouring plants in the same family might also explain the differentiation between different *K* progenies. That such sib-pollination is rather common is indicated by the frequent occurrence of lethal individuals in the progeny after open flowering, a frequency that increases with increased inbreeding. On the other hand, the individuals within the family are generally very different as regards morphological characters, and, therefore, sib-pollination cannot explain the differentiation between *K* progenies.

As regards the height, it may be said that it is on an average, and even in most individual cases, lower in *I* families than in *K* families. This rule is not without exceptions, however. In many cases the differences between *I* and *K* are insignificant. In three cases the *I* progeny is significantly taller than the *K* progeny. In these cases the genotypical height of the mother plants, transmitted to their inbred progeny, must have been greater than that of surrounding plants. In one strain of cocksfoot there is no average difference between I_2 and corresponding *K* families. In this case the mother-plants selected seem to be fairly homozygous as regards height, and thus have already reached their inbreeding minimum.

When *K* families and inbred mother clones are compared, the former are usually the higher, but in several cases the differences are small and insignificant and in two cases *K* is significantly lower than the mother clone. In some cases, then, free pollination has not resulted in any luxuriation, in exceptional cases it may even have the opposite result — facts which have already been discussed.

When inbred progenies are compared with the mother clone the former is in no case significantly higher, in many instances it is signi-

ficantly lower. Only 1 out of 5 I_4 progenies, however, is significantly lower than the mother; here the inbreeding minimum seems to be nearly attained.

It is interesting to note that there are smaller differences between the different *I* progenies or between the different *K* progenies than between the mother clones. Here, evidently, the open pollination has caused the most pronounced luxuriation in the lowest mother plants, thus bringing about a certain equalization. Similarly, the effect of inbreeding has been greatest in the tallest mother plants, resulting also in an equalization. The results are the same after I_2 and I_3 plants from strain *121*. The material is too small to justify any exaggerated generalizations, but it indicates that the most heterozygous plants were to be found among the tallest ones. The results actualize one problem, sometimes overlooked in inbreeding work, viz. the effect of selection upon the results of continued inbreeding. According to current theories the tallest plants should also in general be the most heterozygous ones. Continued selection of extremely tall individuals is therefore liable to delay the increase in homozygosity and to result in a repetition, on the whole, of the same inbreeding results in generation after generation.

On the other hand, according to the dominance theory, homozygous individuals are also to be expected among the tallest ones, and inbred progenies of these individuals should not exhibit any inbreeding degeneration. A continued selection of the tallest individuals ought to bring out such homozygous tall ones, which is corroborated, among others, by the results of KING (1918 a and b), who by constant selection of the most vigorous individuals through many generations was able to breed strains without any degeneration. These strains have most probably been homozygous dominants, and their occurrence offers a striking illustration of the importance of selection in inbreeding work. In many cases, where the initial population is highly heterozygous, several generations will probably be needed, before the expected homozygous dominants are obtained. It is obvious, however, that the homozygosity increases only in the *progeny* of inbred plants, a fact which VALLE seems to have overlooked, when he states (VALLE 1931 b): »Die Variationskoeffizienten zeigen also, dass die Variation der I_1-Generation im Selbstungsmaterial grösser ist als in dem nach freiem Abblühen erhaltenen Material. Es scheint also, als hätte die in einer Generation durchgeführte Selbstung nicht die Homozygotie in bezug auf die vorliegende Ertragseigenschaft vermehrt».

Great and significant differences between the inbreeding effects in

different plants were ascertained. According to the dominance theory, the plants showing the greatest inbreeding effect should be the most heterozygous ones. If this were true, there should be a positive correlation between the effect of inbreeding and the variability in the inbred material. The correlations determined are, however, of a different nature, and must therefore be treated somewhat in detail.

In meadow fescue the correlation is positive, as expected, in cocksfoot the correlation is positive for the material inbred from I_0 to I_1, but negative when the isolated mother plants belong to I_1. In timothy, positive and negative correlations are obtained, but none of them is significant and it has not been possible to get any definite results in this species. In the calculations of these correlations, the effect of inbreeding has been measured by the difference between K and I, and this may explain the varying results. When I_0 plants are openly pollinated by their neighbours in the same population, the progeny may be approximately representative of the mother plant. Thus, an approximately correct estimate of the effect of inbreeding is obtained, and the correlation between this effect and the variability in I_1 is positive, as was to be expected. When the mother plants are I_1 there is already a considerable differentiation between them, and open pollination will result in some luxuriation in the progeny. This luxuriation will be most marked after the most homozygous, *i. e.* the lowest plants, and the apparent effect of inbreeding (K—I) will be negatively correlated with variability in the inbred progeny. This explanation fits in with the result in cocksfoot, and most probably accounts also for the varying results in timothy. Here the varying degrees of inbreeding in different strains and also the mode of planting the material in the field, make it more difficult to compare the correlations with the inbreeding generation and with the errors in the estimate of inbreeding effect. The true inbreeding effect, determined by the aid of mother clones, is ascertained in altogether too few cases to make any determinations of significant correlations possible.

The fact that the various inbreeding phenomena, observed in height, are due to segregation is further proved by the great differentiation in this character. Since no intra-plant variation in height can be determined it is somewhat more difficult to prove genetical differentiation in height than in fertility. The fact that the I families are more variable than the K families is most probably due to segregation. It might be due to greater modificability in I, however, caused by specific effects of the inbreeding, and, therefore, offers no definite proof. It is

of interest to note that in the strain of cocksfoot, in which no inbreeding effect could be ascertained, no difference in variability between *I* and *K* could be found either.

When clones of the mother plants are available it is possible to estimate the importance of environmental modifications, and when the variability between plants in the progenies is decidedly greater than that between the plantlets in the mother clone, this may be taken as a proof of genetical differentiation between the plants. The genetical differentiation between plants in the same family could be demonstrated still further in one I_1 family of timothy, in which all plants were vegetatively propagated, and measurements were made in two different years. The variation was decidedly greater between the clones than within the clones. The correlation between the heights in the two years has been determined, and then the non-correlated variability in both years. This uncorrelated variability is about the same in both years, and is significantly greater than the variability between plantlets in the clones.

The plants were divided and moved after the first measurement was made. The correlation found cannot therefore, as has been discussed previously (page 124), depend upon parallel modifications, but gives a minimum estimate of genetical differentiation between the plants. The fact that the uncorrelated variability is greater than that within the clones may have two explanations. The mode of reaction of the plants may have been different in the two years, and such differences may partly be due to the effect of division and transplantation. On the other hand, the environmental differences may be greater between the different clones than between plantlets within the clones. As each clone was planted in a short row, those rows being arranged after one another in the field, the latter explanation seems very probable, and at any rate the material cannot be utilized to prove any different reactions in different years.

The inbreeding effect in different generations. — The dominance theory as generally accepted presumes that the effect of inbreeding should be greatest in the first generation, and then gradually diminish in geometrical progression. As has been pointed out by RASMUSSON (1933), this need not necessarily be the rule, but the »inbreeding curve» may be dependent on the number of factors and the »coefficient of interaction». Many factors and a low coefficient of interaction tend to delay the phenotypic effect of inbreeding until rather late generations. On the other hand, the absolute effect of inbreeding in different generations depends on the constitution of the initial plant. As the different

generations of inbreeding in the present investigation are not derived directly from one another, but represent different initial populations or different selections within the same population, nothing can be said about the course of inbreeding in successive generations. The only observation bearing upon this problem is the very scanty effect of inbreeding from I_3 to I_4 in strain *121*, which may indicate that in this material at least, the inbreeding minimum is rather easily obtained.

Skewness in inbred material. — EMERSON and EAST (1913) used the symmetrical distribution in inbred material as an argument against the dominance theory. FISHER et al. (1932) have shown, however, that some of the distributions of EMERSON and EAST are, in reality, somewhat skew. COLLINS (1921) has also pointed out that with many segregating cumulative factors the skewness may be inappreciable, and RASMUSSON (1933) has further studied the influence of the number of factors and the size of the »coefficient of interaction» upon the skewness. In the present investigation the skewness increased very markedly with increased inbreeding. I_0 material did not show any skewness in the progeny, either after isolation or after open pollination. The I_1 and I_2 material studied is not directly comparable to the I_0, since they are derived from different strains. The two later inbred generations are, however, from the same strain, and the fact that skewness in the progeny, inbred and cross-bred, increases from I_1 mother plants to I_2 mother plants is therefore of great significance, and also strengthens the value of the difference between I_0 and the others. Since the continued inbreeding is assumed to decrease the number of heterozygotic factors, the results are in complete agreement with the theories and with the assumptions of COLLINS and RASMUSSON. The same is true of the fact that the differences between different families as regards skewness increase with inbreeding, since the differences in heterozygosity are expected to be relatively more important in inbred material. The skewness in the *K* progenies is again an example of the influence of the constitution of the mother, but may also be due to pollination by nearly related neighbours, resulting in a high degree of homozygosity even in cross-bred progeny. The *K* progenies are not so skew as the inbred ones, however, and the difference increases with inbreeding, which is again in full agreement with the theories.

Correlations between different characters in inbred material. — In the I_1 family of timothy already mentioned, where all plants were clonally propagated, exact measurements were taken of several characters besides the height, and the correlations between the different

characters were determined. Panicle length, tillering and fertility were all positively correlated with the height, but there were also indications that at least some of these characters varied, too, independently of the height. If the common correlation with the height was eliminated, there was no partial correlation between panicle length and tillering, nor between panicle length and fertility. If linkage had been the cause of the correlation, it is difficult to understand why the other characters should not also show independent partial correlation. Most probably, therefore, the correlated variation is to be considered as a variation in general vitality. Weak plants are poorly developed in all respects, even if the different characters studied are not generally correlated. The very wide variation observed in this family is, therefore, probably not due to segregation in factors influencing mainly separate characters but in factors with a deep-going effect on the whole development of the individual. Possible factors with more specific influences are suppressed by the vitality factors and cannot exercise any influence of importance.

Similar correlations have been determined in *I* and *K* progenies of two I_2 plants of timothy. Panicle length and tillering are positively correlated with the height in inbred as well as in cross-bred progenies. The existence of an independent variation in panicle length is strongly suggested but cannot be proved. In one of the groups panicle length and tillering are more strongly correlated in the *I* family than in the *K* family, which is in agreement with the theory, if we suppose the correlation to be due to variation in general vigour, and the *I* family to be more homozygous as regards the factors determining this vigour. Further, panicle length and tillering are significantly more strongly correlated in one pair of *I* and *K* than in the other, indicating different constitution as regards general vitality factors in the different mother plants. It should finally be mentioned that the partial correlations between panicle length and tillering are widely different in the different groups. In one group the partial correlations are negative, significant in *I*, in the other group they are positive and significant in *K*. These differences must also be ascribed to differences between the mother plants.

Inbreeding depression in separate characters and in general vigour. — It has already (page 138) been mentioned that there is no fundamental difference between partial and general inbreeding depression, both being due to segregation of Mendelian factors. The correlations just discussed show, however, that some of these factors have a rather

»general» effect upon the development of the plants. Besides the correlations just mentioned there is, in the entire material, a significant positive correlation between height and panicle length and between height and general fertility. These correlations show that, in many cases, the effects of inbreeding manifest themselves parallelly in several characters. This is, however, by no means the general rule in the present material. This is proved already by the fact that in some cases where a correlation occurs an independent variation in the different characters is discernible. Further, in a great many cases wide variations in different characters were noted, but no decrease in general vigour could be observed. A striking example is offered by strain *404* (I_2 from *Kämpe*) which is significantly lower than the initial population, but yields more green matter (see page 94). Family 4933 from *Kämpe* offers an example of the opposite kind. In this family there is a strong segregation in general vigour and the different characters measured show very marked correlations.

If the correlations were due to linkage between factors with separate effects they ought most probably to be of about the same strength between all characters. The determinations of partial correlations in family 4933 have shown, however, that all the characters are correlated with height, but that if this common correlation is eliminated, the other characters vary quite independently, a fact that speaks strongly against the assumption of linkage. In these cases, the height must be considered as a good measure of the general vigour, and the correlations are most probably of a physiological nature, caused by genetic factors with a strong influence upon several characters. Such factors with a wide pleiotropic effect form a link between the more specific factors and the sub-lethals and lethals, and together with the latter they may be denoted as »vitality-factors». By »vitality-factors» are, thus, meant such factors as have a fundamental influence upon the development of the plant, and recessive homozygosity in such factors causes a depression in general vitality, sub-lethality or even lethality.

We are, thus, able to distinguish between genes with different effects, qualitatively as well as quantitatively, and the different degrees of inbreeding effect, observed after different mother plants, are due, not only to different *degrees of heterozygosity* of the mother plant, but also to the *nature of the heterozygous factors.* If these have only a more special effect on separate characters no general depression in vigour is observed, but the inbreeding simply brings about a differentiation as regards these characters. If the selfed individuals are

heterozygous as regards »vitality-factors» the results of inbreeding show themselves in a differentiation in general vigour. This differentiation may result in dead seeds, chlorophyll-deficient seedlings, dwarfs and other lethal or sub-lethal individuals, but may also express itself in the occurrence of viable but less vigorous plants, there being a continuous series of variation from total lethality up to normality. Several cases of strong inbreeding effect seem to be explainable by the assumption of vitality factors with great phenotypical effect. In cases where only a weak general depression could be observed the vitality factors have had less importance, and when no such general depression was at hand, all vitality factors of any importance must have been homozygous in the mother individual. The most complicated segregation is obtained in the inbred progeny of individuals, heterozygous in many factors of different nature and importance. The differences between different kinds of inbreeding effect are, however, in no cases of a fundamental nature but must be considered as different gradations of one and the same phenomenon.

It has been maintained above that most, or at any rate an important part of the correlations observed, must be due to the pleiotropic effects of »vitality-factors». It is rather probable, however, that in some cases linkage may occur as a cause of correlations. This explanation seems to be the only possible one, when the partial correlation between panicle length and tillering in one family is significantly positive, in another significantly negative. (Cp. above, page 150).

Different authors, working either with the same species or with different species, have often obtained widely differing results of inbreeding. The results of the present investigation strongly emphasize the fact that such differences are always to be expected and are most probably due solely to differences in the initial material. Different populations, and also different individuals within the same population, give widely different results after inbreeding, and this may be due to different degrees of heterozygosity, but also to the nature of the heterozygous factors. The danger of generalization, even of results gained from a large material, is made obvious by these facts.

As regards the effect of inbreeding, the results of the present investigation are in full accordance with current theories, *i. e.* the dominance theory, as completed with the hypothesis of linkage and the interaction-hypothesis. Inbreeding depression has been shown to be very common in allogamous grasses, but the degree of depression varies widely with the constitution of the mother plant, and all depression

phenomena observed could easily be explained by the assumption of segregating factors. The results are not only in accordance with current theories, but in some instances they could be utilized in disproving objections raised against the dominance theory.

The complicated segregation obtained after selfing within allogamous species is very difficult to analyse exactly. The best way to attack the still unsolved problems of inbreeding seems, therefore, to be extensive experimentation with artificial hybrids of autogamous plants. On such material the detail problems may be more easily clarified, and then it may be possible definitely to solve even the more complicated problems offered by allogamous species.

V. SUMMARY.

1. The purpose of the investigation was to contribute to our knowledge of the fertilization biology, especially the self-fertility, of some economically important herbage grasses, and to study the effect of inbreeding upon the progeny.

2. The fertility has been investigated more or less extensively in the following species: *Festuca pratensis, F. rubra, F. ovina, Poa pratensis, Alopecurus pratensis, Dactylis glomerata, Phleum pratense, Lolium perenne, L. multiflorum, L. remotum* and *L. temulentum*. The effect of inbreeding has been studied mainly in *Phleum pratense, Dactylis glomerata, Festuca pratensis, Lolium perenne* and *L. multiflorum*.

3. The present paper gives detailed results of the investigations in *Festuca pratensis, Dactylis glomerata* and *Phleum pratense*, while the results in other species have been published elsewhere and are only briefly summarized in this paper.

4. Reviews of the experimental results in each species are given on page 26 (*Festuca pratensis*), 39 (*Dactylis glomerata*), 110 (*Phleum pratense*) and 118 (other species).

5. Most of the species investigated have a low average self-fertility, but *Lolium remotum* and *L. temulentum* are highly self-fertile, and *Poa pratensis* has a rather high degree of self-fertility. Great genetical differences between different individuals have been found in most of the species. Exceptions are *Lolium multiflorum, L. temulentum* and *L. remotum*. The two latter species may be completely self-fertile with no differences between individuals.

6. Even as regards general fertility, great differences between indi-

viduals are found in the species investigated. Sterility is often accompanied by a capacity of vegetative propagation (pages 29 and 119).

7. The causes of the variation in fertility have been separated by means of the analysis of variance and by determination of correlations (discussion on pages 124 and 131).

8. The different types of sterility met with have been classified according to the definitions of previous authors (page 123).

9. The relation between »isolation-fertility» and »self-fertility» is discussed (page 128). The former is in general lower than the latter, because of the modifying influences of the isolation. These modifying influences are least marked when comparing different panicles within the same bag, more so between different bags on the same plant, and still more when different plants are compared.

10. The existence of genetical differences in fertility is proved in three different ways, viz. 1) much greater variation between plants than within plants or between plantlets of the same clone, 2) correlations between fertility of the same individuals under different environmental conditions, and 3) correlations between the fertility of the mother plant and its progeny.

11. The occurrence of self-sterility after inbreeding is shown to be due to segregation in different factors, directly causing a decrease in fertility or causing a depression in general vigour, which again impedes the fertility. The marked differentiation as regards fertility indicates the existence of comparatively few but effective genetic factors. Selection in inbred families results in constant sterile types or in constant highly fertile types.

12. A correlation between self-fertility and general fertility could be demonstrated in *Festuca pratensis, F. rubra, Poa pratensis* and *Phleum pratense.* The causes of this correlation have been discussed (page 134). The correlation is not, however, complete, but there is most probably an independent segregation in self-fertility.

13. Deleterious effects of inbreeding have been shown to be very common in the species investigated in this respect, with the exception of *Poa pratensis.* This species, however, is probably not normally sexual. The effects of inbreeding in the self-fertile species *Lolium remotum* and *L. temulentum* have not been studied.

14. Different methods for the determination of the inbreeding effect have been discussed (page 139) and it has been pointed out that wrong methods may lead to great mis-interpretations of the results. In connection with this, the question as to what should be meant by a

material »free from inbreeding» was briefly discussed (page 142). A theoretical I_0 generation is hardly found in nature, and the notations I_0 and I_n in a material are only relative indications of the degree of inbreeding.

15. The relations between »isolation effect» and inbreeding effect are discussed (page 143). It is shown, that in the present material the influence upon the seed of the unfavourable environment within the bags is of minor importance for the development of the inbred progeny.

16. In some cases in *Lolium perenne* the germination is poor after isolation. The low germination per cent. is most likely due to lethal factors, which kill the embryos. Positive correlation exists between the germination in isolated and non-isolated seed from the same plant.

17. Chlorophyll-deficient seedlings, dwarfs and other lethal and sub-lethal types are more common in inbred material than in progenies after open pollination. The winter hardiness is also impeded by inbreeding, which is considered to be due to segregation in factors with a sub-lethal effect.

18. A marked effect of inbreeding upon height could be demonstrated, whether the inbred material was compared with »outbred» progeny or with the mother plant itself. If the mother plants were already inbred, a decrease in height could in general be observed in the inbred progeny, but an increase in height after open pollination. There are exceptions, though, where the »outbred» progeny was lower than the mother plant.

19. There are great differences in height between different families, and these differences are observed in inbred as well as in »outbred» families, although they are generally more marked in the inbred material. The differentiation within the families is strongest in the inbred material, which indicates the occurrence of a segregation in height.

20. The differences existing between mother plants in inbred generations, represented by clones, are diminished after sexual reproduction, inbreeding or open pollination. This fact is discussed and explained in accordance with the dominance theory (page 146).

21. Different plants show widely different effects of inbreeding upon the progeny. The correlations between effect of inbreeding and variability in the inbred material have been determined and discussed (page 147).

23. The differences between successive generations as regards in-

breeding effect could only be studied on a very scanty material. The results indicate that the inbreeding minimum is rather rapidly attained in some timothy strains.

24. The skewness of the distribution has been determined in material belonging to different inbred generations. The skewness increases with increased inbreeding, which fact is discussed in its bearing upon the dominance theory and upon the hypothesis of interaction (page 149).

25. In some cases several different characters are strongly correlated in inbred material. This fact is discussed (page 150) and considered to indicate segregation in »vitality factors» of fundamental importance for the development. In some families, the correlation is probably due to linkage. In many cases, the different characters studied vary independently, which is taken to indicate segregation in factors with a more special effect on separate characters.

26. The differences between different plants as regards the effect of inbreeding upon their progeny is discussed (page 151), and it is pointed out that the constitution of the mother plant decides the result of inbreeding. Differences may be caused by different degrees of heterozygosity but also by the nature of the heterozygous factors. The wide variation in the results of inbreeding makes it impossible to generalize from the results of a single investigation, even if this is made on an extensive material.

27. All results obtained in the present investigation are in full accordance with current theories, *i. e.* with the assumption that all the effects of inbreeding may be explained by Mendelian segregation.

The Västernorrland Substation of Sveriges Utsädesförening, Undrom, Sweden, April 1933.

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ZUR GENETIK VON PHASEOLUS VULGARIS
VII. ZWEI WEITERE GENE FÜR SAMENEIGENSCHAFTEN, Cor UND Fast

VON *HERBERT LAMPRECHT*
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(With a summary in English)

DIE phänotypische Manifestation der beiden hier zu besprechenden Gene ist wohl sicherlich jedem oder wenigstens den meisten bekannt, die sich einigermassen mit dem Studium verschiedener Rassen von *Phaseolus vulgaris* beschäftigt haben. Die eine dieser beiden Eigenschaften betrifft eine gewisse Zeichnung der Testa in unmittelbarer Nähe des Hilumrandes, die andere eine charakteristische Form der Kotyledonen und damit auch des Samens.

Die in Frage stehende Zeichnung der Testa ist von mir früher (LAMPRECHT 1932) erwähnt und als *Corona* bezeichnet worden. Die Corona ist ein farbiger, den Hilumrand umfassender Ring, der an der Stelle der Caruncula — soweit bisher beobachtet — stets unterbrochen ist. An der der Caruncula gegenüberliegenden Stelle aussen am Hilumrand, dem Platz der Mikropyle, ist die Corona entweder geschlossen oder unterbrochen. Letzteres kommt bedeutend seltener vor. Im ersteren Falle macht sie einen kleinen, vom Hilumrand nach aussen vorspringenden Bogen um die Mikropyle und ist an dieser Stelle in der Regel bedeutend schmäler als an den langovalen Seiten des Hilums. An den letzteren Stellen hat die Corona gleiche oder etwas grössere Breite als der Hilumrand. Die Corona kann vom Hilumrand zuweilen durch einen feinen helleren Rand getrennt sein, oder sie kann — was meistens der Fall ist — unmittelbar an den Hilumrand anschliessen und so als eine Fortsetzung dieses nach aussen in einer mehr oder weniger abweichenden Farbe erscheinen. Ein Same mit gefärbtem Hilumrand und typisch ausgebildeter Corona ist in Fig. 1 abgebildet.

Die Farbe der Corona ist eine verschiedene. Bei bestimmten Testafarben oder vielleicht Gruppen von solchen scheinen auch nur bestimmte Coronafarben vorzukommen. Die Farbe der Corona steht also anscheinend in einer bestimmten Beziehung zur genotypischen Konstitution für die Testafarbe.

Reinweisse Samen mit Corona sind von mir noch nicht beobachtet

worden. Offenbar ist demnach für die Ausbildung einer farbigen Corona teils die Anwesenheit von *P*, dem Grundgen für Testafarbe, teils die Anwesenheit irgendeines der sechs Farbgene *C*, *J*, *G*, *B*, *V* oder *R* in dominanter Form erforderlich.

Im Folgenden werden eine Anzahl von Testafarben mit den ihnen entsprechenden Genenformeln sowie den bei denselben vorkommenden Coronafarben angeführt. In bezug auf die Bezeichnung der Testafarben sei auf eine meiner früheren diesbezüglichen Arbeiten (LAMPRECHT 1933, S. 254—259) verwiesen. Die Bezeichnung der Coronafarben erfolgte auf Grund der auch l. c. benutzten Arbeit von R. RIDGWAY (1912): Color Standards and Nomenclature (abgekürzt = CS).

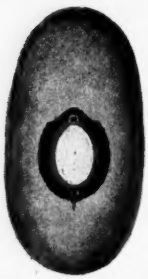

Fig. 1. Ein Samen mit Bister Hilumrand und aussen um diesen mit Dark Olive Corona. Die Corona ist durch die Caruncula unterbrochen und macht einen kleinen schmalen Bogen um die Mikropyle.

Geschwefeltes Weiss, *PP CC jj gg bb vv*; Corona: Dunkles Dusky Green Blue (2), CS XXXIV, 43″ m—n.

Gelblich Weiss, *PP CC jj gg bb vv* (*mimi miamia*?); Corona: Buffy Brown, CS XL, 17‴ i.

Rohseidengelb, *PP cc JJ gg bb vv*; Corona: Helles Ochraceous-Orange, CS XV, 15′—15′ a.

Schamois, *PP CC JJ gg bb vv*; bei dieser Testafarbe sind zwei verschiedene Coronafarben angetroffen worden und zwar: Dusky Yellowish Green bis Dusky Olive-Green, CS XLI, 29‴ m—25‴ m und Ochraceous-Tawny, CS XV, 15′ i.

Maisgelb, *PP cc JJ GG bb vv*; Corona: Yellow Ocher-Orange, eine Farbe, die zwischen Yellow Ocher, CS XV, 17′ und Ochraceous Orange, CS XV, 15′ liegt.

Bister, *PP CC JJ GG bb vv*; Corona: Dark Olive bis Deep Olive, CS XL, 21‴ m—k.

Havannabraun, *PP cc JJ gg BB vv*; Corona: Tawny, CS XV, 13′ i und etwas dunkler bis Hell Hazel, CS XIV, 11′ j—k.

Münzbronze, *PP CC JJ gg BB vv*; Corona: Dunkles Dusky Dull Bluish Green, CS XLII, 4‴ m—n.

Mineralbraun, *PP CC JJ GG BB vv*; Corona: Dull Blue-Green Black, CS XLVIII, 41⁗ m.

Ageratumblau (bis *Hell Zimtfarbig*), *PP cc JJ GG bb VV*; Corona: Clay Color mit Übergängen zu Cinnamon, CS XXIX, 17″—15″.

Graulich Indigo, *PP cc JJ GG BB VV*; Corona: Wood Brown, CS XL, 17‴ und dunkler. Bei dieser und bei der vorigen Testafarbe, *Ageratumblau*, ist die Farbe der Corona heller als die der Testa.

Kastanienbraun, *PP CC JJ GG bb VV*; Corona: Bei dieser Testafarbe

ist — gleichwie bei Reinschwarz anscheinend immer — gewöhnlich keine Corona wahrnehmbar. Mitunter erscheint diese aber in einer helleren Farbe als die der Testa, die dann am ehesten Vinaceous-Brown, CS XXXIX, 5''' i entspricht.

Die vorstehend mitgeteilte Zusammenstellung der bei 12 verschiedenen Testafarben vorkommenden Coronafarben dürfte einstweilen folgende Feststellungen gestatten. Die Farbe der Corona — wenn eine solche überhaupt ausgebildet wird — ist von der genotypischen Konstitution für die Testafarbe abhängig. In den oben mitgeteilten Fällen sind es insbesondere zwei Gene, die in dieser Hinsicht einen starken Einfluss besitzen, nämlich *C* und *J*. Bei sämtlichen Testafarben, die *J* aber nicht *C* in ihrer genotypischen Konstitution haben, finden wir orange-braune Coronafarben. Es sind dies die Testafarben: Rohseidengelb, Maisgelb, Havannabraun, Ageratumblau und Graulich Indigo. Die übrigen drei Gene *G*, *B* und *V* scheinen hierbei keine nennenswerte Rolle zu spielen. Bei Anwesenheit von nur *C* hat die Corona eine dunkel blaugrüne Farbe: Dunkles Dusky Green Blue. In den Fällen wo *C* und *J* gemeinsam vorkommen, scheinen im allgemeinen Farben aufzutreten, die eine gewisse Kombination der für *C* und *J* charakteristischen Farben darstellen, z. B. Dunkeloliv—Olivbraun—Braun. Schliesslich wäre zu erwähnen, dass die Gene *mi* und *mia*, die bei Rohseidengelben Samen für die Ausbildung eines Mikropylenstreifens verantwortlich sind und die überdies Geschwefeltes Weiss in Gelblich Weiss umzuwandeln scheinen, gleichzeitig hiermit auch eine Veränderung der Coronafarbe von Dunkles Dusky Green Blue zu Buffy Green bewirken. Für die Testafarbe Schamois sind zwei Coronafarben festgestellt worden. Vielleicht ist die letztere, Ochraceous-Tawny, durch die beiden eben genannten Gene bedingt, die Geschwefeltes Weiss in Gelblich Weiss verwandeln. Die Testafarbe Schamois scheint durch diese jedoch nicht sicher verändert zu werden.

Was die Vererbung der Corona betrifft, so ist schon früher in mehreren meiner Kreuzungen sowie auch in spontanen Kreuzungen eine Spaltung in Samen mit und ohne Corona beobachtet worden. Eine exakte Analyse ist in diesen Fällen jedoch auf unüberwindbare Schwierigkeiten gestossen, da es stets eine verhältnismässig grosse Anzahl von Individuen — gewöhnlich mit mehr oder weniger dunklen Testafarben — gegeben hat, bei denen einige Samen eine Corona nur schwach angedeutet hatten, andere aber keine Spur einer solchen aufzuweisen schienen. Man war hierbei niemals sicher, ob gewisse Proben nicht doch eine sehr schwache Corona zeigten oder nicht. Andere Indivi-

duen wiederum hatten Samen mit einer sehr starken Corona; und alle Übergangsstufen schienen vorzukommen. Bei den dunklen Testafarben Reinschwarz, Veilchenviolett, Kastanienbraun etc. war aber so gut wie niemals eine Corona wahrnehmbar. Wie wir weiter unten sehen werden, beruhte die schwach ausgebildete Corona, deren Feststellung bei gewissen Testafarben überdies unsicher ist, auf Heterozygotie in der Erbanlage für die Ausbildung der Corona.

Um ein in genannter Hinsicht vollkommen sicher analysierbares Material zu erhalten wurden im Jahre 1931 zwei Linien miteinander gekreuzt, die beide die Testafarbe Geschwefeltes Weiss hatten, die eine mit starker, die andere ohne Spur von Corona. Der eine Elter ist

Fig. 2. Drei Samen mit der Testafarbe Geschwefeltes Weiss (*PP CC*) und weissem Hilumrand. Linker Same ohne Corona, *Cor Cor*, rechter Same mit starker Corona, *cor cor*, in der Farbe Dunkles Dusky Green Blue, mittlerer Same mit schwach angedeuteter Corona, *Cor cor*, in gleicher Farbe.

Linie 23 aus der Handelssorte Pariser Gelbe, mit starker Corona in der Farbe Dunkles Dusky Blue (siehe Fig. 2, rechter Same), der andere Elter ist die schon früher mehrmals verwendete Linie 29 aus der Handelssorte de la Chine, ohne Corona (siehe Fig. 2, linker Same).

Die Kreuzung, Nr. 83, ist in beiden Richtungen ausgeführt worden, und in beiden Fällen ist das gleiche Resultat erhalten worden. Die auf der ersten Generation erhaltenen Samen haben durchweg eine mehr oder weniger schwache Corona in der gleichen Farbe wie der eine Elter, Linie 23, gezeigt. Der mittlere Same in Fig. 2 stellt einen solchen Hybridsamen dar. Die Stärke der Corona zeigte hier eine gewisse Variation, die offenbar modifikativer Natur ist. Sie trat auch so gut wie immer an den Samen ein und derselben Pflanze auf. Aber niemals erreichte die Farbe der Corona auch nur annähernd die Stärke derjenigen der Linie 23. Die Samen einiger Pflanzen wurden überdies — was bei

einem Selbstbefruchter wie *Phaseolus vulgaris* wohl überflüssig erscheinen dürfte — in solche mit sehr schwacher, schwacher und deutlicherer Corona sortiert und gesondert ausgesät. Das Resultat in F_2 ist jedoch dasselbe gewesen.

Das in der zweiten Generation festgestellte Spaltungsresultat ist in Tabelle 1 wiedergegeben. Das hier spaltende Genpaar wird, abgeleitet

TABELLE 1. *Die Spaltung im Genpaar Cor—cor in F_2 von Kreuzung 83.*

Familien-Nr.	Anzahl Individuen			Summe Individuen
	ohne Corona	mit schwacher Corona	mit starker Corona	
7271/1	20	35	15	70
7271/2	13	28	10	51
7272/1	16	20	12	48
7272/2	23	54	28	105
7273/1	19	42	10	71
7273/3	13	29	12	54
7274/1	5	8	4	17
7274/2	7	13	6	26
7275/1	8	21	14	43
7275/2	9	16	8	33
7275/3	9	19	13	41
7277/1	8	23	13	44
Summen:	150	308	145	603
Erwartet:	150,75	301,50	150,75	—
D/m für 1:2:1	0,07	0,53	0,54	—

von Corona, als *Cor—cor* bezeichnet, und es soll die doppeltrezessive Form *cor cor* der starken Corona entsprechen. Wie aus Tab. 1 ersichtlich wurde eine klar monohybride Spaltung nach dem Verhältnis 1 *CorCor* : 2 *Corcor* : 1 *corcor* erhalten. Die gefundenen Zahlen zeigen sehr gute Übereinstimmung mit den theoretisch erwarteten. Die Klassifikation hat in dieser Kreuzung keinerlei Schwierigkeiten verursacht. Es bestand niemals der geringste Zweifel darüber, ob keine oder nur eine schwache Corona vorhanden war. Unter den Samen mit schwacher Corona gab es dagegen mitunter einzelne, die sich in der Stärke der Farbe recht sehr denen mit starker Corona näherten. Es waren dies aber dann nur einige Samen einer Pflanze und nicht alle.

Mit Hinblick auf diese Erscheinung ist es leicht zu verstehen, dass eine exakte Analysierung dieser monohybriden Dreitypen-Spaltung (sog. *Zea*-Spaltung) in Kreuzungen, wo überdies mehr oder weniger

dunkle Testafarben ausspalten, auf praktisch genommen unüberwindbare Schwierigkeiten stossen wird. Ein Studium der Vererbung der verschiedenen Farbgene für Testafarbe zusammen mit dem Genpaar *Cor—cor* wird aber trotzdem möglich sein, nur müssen hierzu eben Elternlinien verwendet werden, die immer Träger nur je eines Farbgens sind. Jedes der sechs Farbgene für die Ausbildung der Testafarbe bei *Phaseolus vulgaris* verursacht nämlich nur eine ganz helle Farbe (siehe LAMPRECHT 1933, S. 250—251).

Hier mag schliesslich erwähnt werden, dass die vier bisher analysierten Zeichnungen in der Nähe des Hilumrandes bei *Phaseolus vulgaris* eine recht verschiedene Vererbungsweise zeigen. Der Carunculastrich (Genpaar *Ca—ca*) zeigt anscheinend vollkommene Dominanz, die Bräme (Genpaar *Mar—mar*) ist eine rezessive Eigenschaft, der Mikropylenstreifen (Genpaare *Mi—mi* und *Mia—mia*) erscheint doppelt rezessiv bedingt und die hier oben analysierte Zeichnung, die Corona (Genpaar *Cor—cor*), zeigt eine monohybride Spaltung, bei der der Heterozygot eine intermediäre Stellung einnimmt (vgl. LAMPRECHT 1932 und 1933).

Fig. 3. Ein typischer Same vom *fastigiata*-Typus aus Linie 34 der Handelssorte Tausend für Eine (= Zucker-Reisperl).

Die zweite Sameneigenschaft, deren Vererbung hier studiert werden soll, bezieht sich auf die Form der Kotyledonen und damit auch auf die der Samen. Unter den Hunderten von Handelssorten der Gartenbohne nimmt die kleine Perlbohne Tausend für Eine (auch Zucker-Reisperl genannt) auf Grund ihrer charakteristischen Samenform eine Sonderstellung ein. Fig. 3 zeigt einen für diese Sorte typischen Samen. Wie ersichtlich hat dieser Same eine schräg zugespitzte Form. Die Spitze liegt links, auf der Mikropylenseite, aber nicht in der Mitte des Samenendes sondern recht stark nach unten zur Basislinie verschoben. Auf dieser Seite fällt der Samen gleich von der Mikropyle an stark ab. Die abfallende Linie ist schwach bogenförmig gekrümmt. Im Zusammenhang hiermit lässt sich feststellen, dass solche Samen auf der Mikropylenseite des Hilumrandes fast stets grössere Höhe aufweisen als auf der Carunculaseite, und ferner dass die Basislinie des Samens keine symmetrische Krümmung mit dem tiefsten Punkte etwa in der Mitte aufweist sondern dass letzterer gewöhnlich recht deutlich gegen das spitze Ende verschoben ist.

Die bei diesem *fastigiata*-Typus, wie ich ihn nennen will, vorhan-

dene schräge Zuspitzung scheint bei so gut wie allen anderen Formen von Bohnensamen durch ein ziemlich regelmässiges, breit gerundetes Ende ersetzt zu sein. Eine Ausnahme hiervon bilden jedoch die an ihren Enden mehr oder weniger abgestumpften und daher eckigen *truncatum*-Samen, die ihre Form dem Umstande zu verdanken haben, dass die Samen noch bei beginnender Reife so dicht in den Hülsen sitzen, dass ihre Enden aneinandergepresst liegen. Von extremen *truncatum*-Samen bis zu den gewöhnlichen Formen mit normal gerundeten Enden gibt es alle Übergänge. Die erblichen Voraussetzungen für die Ausbildung von *truncatum*-Samen werden in zweierlei Richtungen zu suchen sein: teils in der Grösse des Abstandes der Samenanlagen in der Hülse und teils in der Länge der Samen. *Truncatum*-Samen werden also zustandekommen, wenn die Samenlänge den Abstand zwischen den einzelnen Ansatzstellen dieser in der Hülse überschreitet. Fig. 4 zeigt einige verschiedene *truncatum*-Samen, die in F_3 von Kreuzung 21 (siehe weiter unten) ausgespaltet haben.

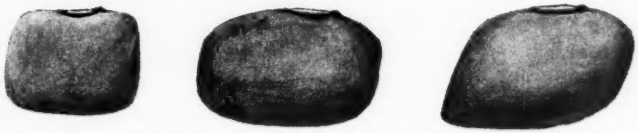

Fig. 4. Drei verschiedene *truncatum*-Samen, ausgespalten in Kreuzung 21. Der rechte Same ist stark schief zugespitzt und gehört dem *fastigiata*-Typus an.

Es ist zu erwarten und auch eingetroffen, dass in Kreuzungen, in denen *truncatum*-Samen auftreten, eine Klassifikation eines Teiles dieser mit Hinsicht auf den *fastigiata*-Typus nicht ganz sicher ist. Eine durchweg sichere Analyse der Vererbung des *fastigiata*-Typus wird also entweder nur in Kreuzungen durchführbar sein, in denen keine *truncatum*-Samen ausspalten, oder auch man ist genötigt eine umfangreiche nächste Generation aufzuziehen um auf Grund der Spaltung in den Familien dieser die Resultate in der vorherigen Generation überprüfen und berichtigen zu können. Letzteres ist aber wohl stets der Fall, da ja zur Beurteilung der Spaltung sonstiger Eigenschaften eine F_2 gebaut werden muss und diese gibt schon F_3-Samen, die dann in teils konstante und (eventuell verschieden) spaltende Familien klassifiziert werden können.

Über die Vererbung der *fastigiata*-Samenform liegt bisher nur eine kurze Mitteilung von E. v. TSCHERMAK (1922, S. 40—41) vor, die er gelegentlich eines Berichtes über die Vererbung des Samengewichtes in

der Kreuzung Zucker Reisperl (Tausend für Eine) × Anker macht. Erwähnt sei, dass Anker lange, walzliche Samenform hat. Über die Form der F_1-Samen wird nichts mitgeteilt. E. v. TSCHERMAK sagt: »Bezüglich der Samenform ist ebenso wie bezüglich des Samengewichtes augenscheinliche Mischsamigkeit an F_1-Pflanzen in der SG_{II} sowie an gewissen F_2-Pflanzen in SG_{III} zu beobachten». Das heisst: die Samen der SG_{II} (= Samengeneration II, die auf F_1 erhaltenen F_2-Samen) zeigten teils walzliche und teils eckige Form und gleiches gilt für die Samen gewisser F_2-Pflanzen. E. v. TSCHERMAK klassifizierte die an zusammen drei F_1-Pflanzen erhaltenen Samen in folgender Weise:

a) 58 reine eckige Reisperlform,
b) 76 intermediär, mehr eckig,
c) 203 intermediär zwischen eckig und walzlich,
d) 75 intermediär, mehr walzlich,
e) 36 reine walzliche Ankerform.

Summe: 448 Samen.

Dieses gefundene Spaltungsverhältnis: 58 a) : 76 b) : 203 c) : 75 d) : 36 e) deutet E. v. TSCHERMAK als etwa 7 : 9 : 32 : 11 : 5 entsprechend (Kombinationszahl 64), also als trifaktoriell.

Die Samen einer der drei F_1-Pflanzen wurden — gesondert nach den oben angeführten 5 Gruppen — in F_2 weitergebaut und ergaben 89 Pflanzen. In bezug auf die hierbei erhaltenen Resultate sagt E. v. TSCHERMAK: »Sonach waren von den phänotypisch in SG_{II} als rein eckig klassifizierten 12 (daneben 8 nicht aufgegangen) Samen nur zwei Drittel homozygotisch, ein Drittel heterozygotisch — für die als rein walzlich klassifizierten acht Samen ergab sich das Verhältnis drei Viertel zu ein Viertel. Umgekehrt erwiesen sich von den äusserlich als intermediär klassifizierten Samen nicht wenig (6 + 12) als genotypisch rein eckig bzw. (13 + 8) als genotypisch rein walzlich. Die rein phänotypische Klassifizierung erweist sich sonach als weitgehend unzuverlässig: ein Gleiches gilt von der Aussage über teilweises Fortspalten äusserlich rein eckiger oder rein walzlicher Samen. Nur das kann erschlossen werden, und zwar speziell aus dem anscheinenden Bestehen recht verschiedener Spaltungsverhältnisse der Heterozygoten (12 : 4, 11 : 5, 9 : 7) — dass eine mindestens trifaktorielle Grundlage für den Unterschied von eckiger und walzlicher Samenform anzunehmen ist». Eigentümlich erscheint es, dass E. v. TSCHERMAK in der 3. Samengeneration wohl die eben genannten drei verschiedenen Spaltungsverhältnisse für eckig: walzlich (nicht umgekehrt!), aber nichts mehr von

dem in der 2. Samengeneration konstatierten ungewöhnlichen Spaltungsverhältnis findet. Theoretisch wäre doch dieses Verhältnis in grösster Frequenz zu erwarten gewesen.

Von mir ist die Vererbung der *fastigiata*-Form in mehreren Kreuzungen studiert worden. Diese haben bisher übereinstimmende und an-

Fig. 5. Links F_1-Same nach Kreuzung Linie 34 (*fastigiata*-Typus) ♀ × Linie 25 (ovaler Typus) ♂, rechts F_1-Same nach reziproker Kreuzung. Letzterer ist in der Form von den Samen der Linie 25 nicht sicher zu unterscheiden.

scheinend eindeutige Resultate geliefert. Der eine Elter ist in sämtlichen Kreuzungen Linie 34 aus Tausend für Eine gewesen. Hier seien kurz die Ergebnisse von 3 Kreuzungen angeführt.

In Kreuzung 21 wurde Linie 34 mit Linie 25 aus Braune Bohne

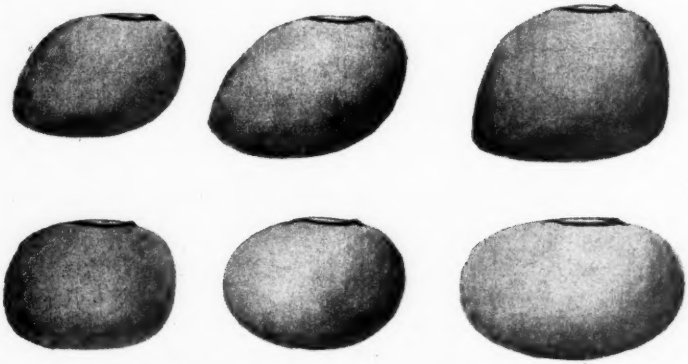

Fig. 6. Sechs verschiedene F_2-Samen aus Kreuzung 21. Obere Reihe drei verschiedene *fastigiata*-Samen; untere Reihe linker Same von unsicherem Formtypus, die beiden rechten Samen von ovaler Form.

(Prinzess-Typus) und umgekehrt gekreuzt. Bei den nach Befruchtung von Linie 34 mit Pollen von Linie 25 erhaltenen F_1-Samen ist jede Spur der für erstere Linie charakteristischen *fastigiata*-Form verschwunden. Die F_1-Samen zeigen anstatt dessen, wie aus Fig. 5 hervorgeht, eine fast ganz symmetrische, länglich ovale Form. Die ovale Samenform scheint

also vollkommen über die *fastigiata*-Form zu dominieren. Wird umgekehrt Linie 25 mit Pollen von Linie 34 befruchtet, so werden F_1-Samen erhalten, die sich kaum in irgendwelcher Hinsicht — vielleicht abgesehen von einem geringen Grössenunterschied — von den Samen

TABELLE 2. *Die Spaltung im Genpaar Fast Fast an F_2-Samen, erhalten auf der ersten Generation von Kreuzung 21: L 25, Braune Bohne × L 34, aus Perlbohne Tausend für Eine.*

Familien- und Pflanzen-Nr.	Anzahl Samen		Summe Samen
	Ovaler Typus: *Fast Fast* und *Fast fast*	Schräg-spitzer Typus: *fast fast*	
10151/1	96	46	142
10152/1	133	46	179
10152/2	124	41	165
10152/3	121	36	157
10153/1	87	31	118
10153/2	171	52	223
10154/1	215	80	295
10154/2	64	28	92
10155/1	103	32	135
10155/2	115	39	154
10156/1	142	54	196
10156/2	97	28	125
10157/1	111	38	149
10157/2	72	28	100
10157/3	90	32	122
10158/1	117	41	158
10159/1	91	34	125
10159/2	60	19	79
10160/1	69	20	89
10160/2	109	38	147
Summen:	2187	763	2950
Erwartet:	2212,50	737,50	—
D/m für 3:1	1,08	—	—

der Linie 25 unterscheiden lassen. Es werden also hier — wenigstens was die Grösse der Samen betrifft — bei reziproker Befruchtung ganz verschiedene Resultate erhalten. Diese bilden offenbar einen Kompromiss zwischen dem Einfluss des fremden Pollens und dem Einfluss der Mutterpflanze auf den Samen. Letztere, hauptsächlich die Samengrösse betreffende Erscheinung, über die von E. v. TSCHERMAK (1922)

eingehend berichtet wird, soll in einer besonderen Arbeit studiert werden.

Die auf der F_1-Generation erhaltenen F_2-Samen zeigten eine Spaltung in verschiedene Form und Grösse. Was die Samenform betrifft, so fand hier hauptsächlich eine Spaltung in rein ovale und *fastigiata*-Typen statt. Sowohl der ovale wie der *fastigiata*-Typus zeigten eine gewisse Variation. Ausser solchen gab es eine geringere Anzahl von Samen, in bezug auf die man im Zweifel verblieb, welchem von diesen beiden Typen sie zugerechnet werden sollten. Fig. 6 zeigt sechs F_2-Samen aus Kreuzung 21. Die drei Samen in der oberen Reihe gehören zweifellos dem *fastigiata*-Typus an, der linke Same in der unteren Reihe

TABELLE 3. *Die Spaltung der F_3-Familien in bezug auf das Genpaar Fast—fast in Kreuzung 21: L 25 Braune Bohne × L 34, aus Perlbohne Tausend für Eine.*

F_2-Familien-Nr.	*Fast Fast*-Familien (konstant)	*Fast fast*-Familien (spaltend)	*fast fast* Familien (konstant)	Summe Familien
7021	39	82	54	175
7022	17	37	21	75
7023	22	33	15	70
7024	17	40	20	77
7025	20	53	19	92
Summen:	115	245	129	489
Erwartet:	122,25	244,50	122,25	—
D/m für 1 : 2 : 1 =	0,76	0,05	0,70	—

ist in bezug auf seinen Typus unsicher, die beiden rechten sind ovale Typen. Die Anzahl in bezug auf den Typus unsicherer Samen erreichte nur wenige Prozent und würde das gefundene Spaltungsverhältnis kaum nennenswert verändert haben können. Da jedenfalls, wie früher erwähnt, eine zweite Generation gebaut und dann die F_3-Samen klassifiziert wurden, konnten eventuelle Irrtümer berichtigt werden. Hierbei wurden die in Tabelle 2 mitgeteilten Zahlen erhalten, die eine klar monohybride Spaltung nach dem Verhältnis 3 ovale : 1 *fastigiata* anzeigen. Das hier spaltende Genpaar bezeichne ich unter Bezugnahme auf den rezessiven *fastigiata*-Typus mit *Fast—fast*.

Eine sichere Bestätigung dafür, dass es sich hier um eine monohybride Spaltung im Genpaar *Fast—fast* handelt, bildet das Resultat der Klassifikation der Samenfamilien in F_3. Die hierbei erhaltenen

TABELLE 4. *Die Spaltung im Genpaar Fast fast an F_2-Samen, erhalten auf der zweiten Generation von Kreuzung 20: L 7, aus Alabaster I × L 34, aus Perlbohne Tausend für Eine.*

Familien-Nr.	Anzahl spaltende Pflanzen	Anzahl Samen		Summe Samen	D/m für 3 : 1
		Ovaler Typus: *Fast Fast* und *Fast fast*	Schräg-spitzer Typus: *fast fast*		
11191	40	3413	1123	4536	0,38
11192	63	4129	1431	5560	1,27
11193	23	1464	463	1927	0,99
11194	4	262	81	343	0,59
11195	31	2441	807	3248	0,20
11196	28	1645	518	2163	1,13
11197	25	1523	517	2040	0,36
11198	40	2111	749	2860	1,47
11199	12	770	309	1079	2,75
11200	1	46	15	61	0,07
11201	7	354	114	468	0,32
11202	12	631	213	844	0,16
11203	19	1151	378	1529	0,25
11204	31	1585	501	2086	1,05
11205	26	1369	458	1827	0,07
11206	21	953	329	1282	0,55
11207	4	152	57	209	0,76
11208	2	111	35	146	0,29
11209	21	1360	474	1834	0,84
11210	13	639	182	821	1,87
11211	3	243	53	296	2,82
11212	11	546	172	718	0,65
11213	17	1112	335	1447	1,62
11214	9	518	180	698	0,48
11215	28	1688	550	2338	0,46
11216	35	1659	529	2188	0,89
11217	3	140	48	182	0,17
Summen:	—	32015	10621	42636	—
Erwartet:	—	31977,0	10659,0	—	—
D/m für 3 : 1..	—	0,31	—	—	—

Zahlen zeigt Tabelle 3. Aus dieser ist ersichtlich, dass insgesamt 489 Familien klassifiziert wurden und diese zeigten in sehr guter Übereinstimmung mit der Erwartung eine Spaltung nach dem Verhältnisse

n *Fast Fast* : 2n *Fast fast* : n *fast fast.*

Die Werte für D/m sind für dieses Verhältnis signifikativ.

Eine Untersuchung der F_2- und F_3-Samen in zwei weiteren Kreuzungen, Nr. 20 und Nr. 41, hat zu gleichen Ergebnissen geführt. Die Kreuzung 20 wurde ausgeführt zwischen Linie 34 aus Tausend für Eine und Linie 7 aus Alabaster I. Die an den F_3-Samen erhaltenen Spaltungszahlen sind in Tabelle 4 mitgeteilt und zeigen ein einwandfreies monohybrides Spaltungsverhältnis an. Kreuzung 41 wurde ausgeführt zwischen Linie 34 und Linie 29 aus de la Chine. In dieser Kreuzung sind bisher nur die F_2-Samen untersucht worden, und auch diese haben ein Spaltungsverhältnis, 3 *Fast* : 1 *fast* entsprechend, geliefert.

In diesen Kreuzungen haben ausser dem Genpaar *Fast—fast* sicherlich noch ein oder mehrere andere die Form beeinflussende Genpaare gespalten. Diese haben aber offenbar bei weitem keinen so markanten Effekt auf die Form wie das Genpaar *Fast—fast*. Die Wirkung des letzteren konnte also in den von mir untersuchten Fällen meistens mit Sicherheit beurteilt werden. In bezug auf die Beurteilung sei nochmals hervorgehoben, dass ausser der direkten Beurteilung von F_2 stets auf Grund der Samenfamilien in F_3 rückgeschlossen werden soll um ev. Irrtümer berichtigen zu können. Technisch ist es ferner bei der Klassifikation sehr von Vorteil, wenn die Samen jeder Probe (Familie) mit regelmässigen Abständen auf einer einen scharfen Kontrast bildenden Unterlage ausgebreitet werden.

In den von mir untersuchten Kreuzungen ist es also nicht zu den grossen Schwierigkeiten bei der Klassifikation der *fastigiata*-Form gekommen wie in der von E. v. TSCHERMAK untersuchten Kreuzung. In meinen Kreuzungen hat aber keiner der Eltern die lange walzliche Samenform gehabt wie die von E. v. TSCHERMAK verwendete Sorte Anker. Es hat also den Anschein, als ob die lange walzliche Samenform durch Gene bedingt würde, die die phänotypische Manifestation des *fastigiata*-Gens mehr oder weniger verhindern. Vielleicht würde auch in diesen Fällen auf Grund eines Studiums der Samenfamilien in der oder den folgenden Generationen eine Klassifikation möglich sein, eine Frage, die ich künftig zu beantworten versuchen werde.

SUMMARY.

1. In a *Phaseolus*-cross the inheritance of the corona, a coloured margin outside the hilum margin (fig. 1), was investigated.

2. The production of the corona is due to the gene *cor*. Seeds with

Cor Cor have no corona, with *cor cor* a very deeply coloured one, and with *Cor cor* a pale coloured corona (fig. 2, table 1).

3. In some other *Phaseolus*-crosses the inheritance of the *fastigiata*-type of the seeds (see fig. 3) was investigated.

4. The production of the *fastigiata*-type is due to the genotypical constitution *fast fast*. The gene *Fast* showed apparently complete dominance. Slight difficulties with regard to the classification of the F_2-seeds were easily eliminated by the study of the F_3-seeds (tables 2 and 4).

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ZUR GENETIK VON PHASEOLUS VULGARIS

VIII. ÜBER FARBENVERTEILUNG UND VERERBUNG DER TEILFARBIGKEIT DER TESTA

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(With a summary in English)

EINLEITUNG.

DIE vorliegende Arbeit ist als erste Mitteilung einer allseitigen und eingehenden Untersuchung der Vererbung der Teilfarbigkeit der Testa von *Phaseolus vulgaris* gedacht. Als Einleitung soll zuerst eine Übersicht über die mir aus Literatur und eigenen Untersuchungen bisher bekannten Typen bzw. Gruppen von Typen mit verschiedener Verteilung der Farben auf der Testa gegeben werden. Anschliessend an diese soll eine Besprechung und Zusammenfassung der bisher über die Vererbung der Teilfarbigkeit veröffentlichten Resultate folgen (Historik), woran ich eine kurze Diskussion der genotypischen Unterlage und der Bezeichnung der bekannten in Frage kommenden Genpaare anschliessen werde.

Es soll hier schon vorweg erwähnt werden, dass die in meinen Kreuzungen erhaltenen Resultate einen Reichtum an teilfarbigen Typen von *Ph. vulgaris* aufweisen, der mit Hinsicht auf die früher in der genetischen Literatur mitgeteilten Ergebnisse und die im Handel bekannten Typen nicht geahnt werden konnte. Ja, es fragt sich, ob wir hier — bei weiteren Untersuchungen — nicht eine Mannigfaltigkeit an Typen finden werden, die derjenigen der Testafarben gleich- oder wenigstens nahekommt. Damit können für *Ph. vulgaris* auch mehrere neue Genpaare festgestellt werden.

Über die Verteilung der Farben auf der Samenschale von *Ph. vulgaris* im allgemeinen ist bisher etwa folgendes bekannt. Die Testa kann entweder reinweiss, d. h. frei von Pigment, oder in verschiedener Weise gefärbt sein. Die gefärbten Typen können je nach der Verteilung der Farbe (oder der Farben) in eine Anzahl gut gegeneinander abgegrenzte Gruppen eingeteilt werden. Zunächst können wir hier zwei Hauptgruppen unterscheiden, nämlich 1) *ganzfarbige* und 2) *teilfarbige* Typen. Bei den ganzfarbigen Typen sind eine oder mehrere Farben über die ganze Testa verbreitet oder verteilt, bei den teilfarbigen da-

gegen ist stets ein gewisser, mehr oder weniger grosser Teil der Testa reinweiss.

Den teilfarbigen Typen sind also nicht jene zuzurechnen, bei denen die Testa auf reinweissem Grunde in irgendeiner Weise eine Marmorierung aufweist, die sich über die ganze Testa erstreckt, denn bei diesen Typen ist nicht *ein gewisser* Teil reinweiss sondern weisse und farbige Flecken beziehungsweise Streifen sind über die ganze Testa zerstreut.

1. *Ganzfarbige Typen.* Diese können wiederum in zwei Untergruppen eingeteilt werden, nämlich a) *einfarbige* und b) *mehrfarbige Typen.*

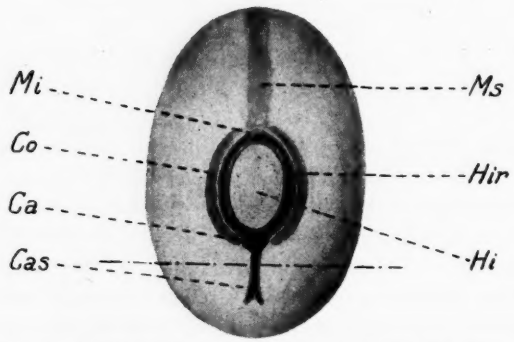

Fig. 1. Abbildung einer Bohne, verschiedene Elemente bzw. Zeichnungen der Testa veranschaulichend. Hi = Hilum (Nabel), Hir = Hilumrand, Ca = Caruncula (Strophiola, Nabelwarze), Cas = Carunculastrich, Mi = Mikropyle, Ms = Mikropylenstreifen, Co = Corona. Die strichpunktierte Linie deutet die Lage eines Schnittes zur Untersuchung des Carunculastriches an, was hier ohne Belang ist.

a) *Einfarbige Typen.* Bei diesen zeigt die ganze Testa mit Ausnahme des Hilumrandes und eventueller, in unmittelbarer Nähe desselben vorhandener Zeichnungen eine einheitliche Färbung. Die Färbung des Hilumrandes wird, soweit bisherige Untersuchungen (siehe LAMPRECHT 1933, S. 250—252) gezeigt haben, durchweg durch einen pleiotropen Effekt der die Farbe der Testa im übrigen bedingenden Gene verursacht. Von den anschliessend an den Hilumrand vorkommenden, begrenzten Zeichnungen seien hier folgende, von mir bisher genetisch untersuchte, angeführt: Carunculastrich, Corona, Margo und Mikropylenstreifen (siehe LAMPRECHT 1932 b, 1933 und 1934 sowie Fig. 1 oben). Diese Zeichnungen (Merkmale oder Abzeichen, wie man sie auch nennen kann) werden, wie in den eben zitierten Arbeiten nachgewiesen worden ist, durch besondere Genpaare bedingt. Die Ausbildung gewisser von ihnen ist jedoch von dem Vorhandensein gewisser Farbgene und damit Testafarben bedingt, worauf bei der hier vorgenommenen Gruppierung indessen nicht Rücksicht genommen werden soll. Die Anzahl dieser Zeich-

nungen ist mit den vier oben angeführten sicherlich nicht erschöpft; ich kenne einige weitere, die gegenwärtig darauf untersucht werden, ob und ev. in welchem Ausmasse sie modifikativ oder erblich bedingt sind. Was oben in bezug auf das Auftreten von Hilumrand und der genannten Zeichnungen für die einfarbigen Typen gesagt worden ist, hat — soweit bisher bekannt — auch für die folgenden Gruppen von ganzfarbigen bzw. teilfarbigen Typen Gültigkeit.

b) *Mehrfarbige Typen.* Bohnensamen, bei denen eine gewisse Zone der Testa eine Farbe, der übrige Teil ein andere aufweist oder überhaupt bei denen die Testa in mehrere Zonen mit zwei oder mehr verschiedenen Farben eingeteilt ist, scheinen nicht bekannt zu sein. Bei den bekannten mehrfarbigen Typen scheinen die Farben nur in der Form von Marmorierung, Bänderung oder gleichsam fein verspritzt vorzukommen. Bei einer Einteilung der mehrfarbigen Typen in verschiedene Untergruppen kann von zwei Gesichtspunkten ausgegangen werden. Teils kann von der Anzahl vorhandener Farben ausgegangen werden, also mit einer primären Einteilung in 2-, 3- u. s. w. farbigen Typen, teils kann primär eine Einteilung in Gruppen mit verschiedenen Zeichnungstypen (Marmorierung etc.) stattfinden und erst sekundär eine Berücksichtigung der Anzahl vorhandener Farben erfolgen. Hier soll der letztere Weg gewählt werden. Die mehrfarbigen Typen können hiernach primär eingeteilt werden in:

I. *Marmorierte Typen*;
II. *Gebänderte* (*gestreifte*) *Typen*;
III. *Gespritzte* (*ungleichmässig punktierte*) *Typen.*

Die *marmorierten Typen* können des weiteren in zwei Serien eingeteilt werden, die phänotypisch eine recht ähnliche Variation aufweisen, aber durch eine ganz verschiedene genotypische Konstitution bedingt werden. In der einen Serie wird die Marmorierung bedingt durch Heterozygotie im Genpaar *C*—*c*, in der anderen durch den Marmorierungsfaktor *M*. Erstere bezeichne ich, da sie keine konstanten marmorierten Nachkommen geben können als Heterozygotmarmorierte, (*Cc*), letztere im Gegensatz hierzu als Homozygotmarmorierte (*MM*). In Fig. 2 sind drei heterozygotmarmorierte Samen abgebildet. Fig. 3 zeigt zwei homozygotmarmorierte Samen. Diese könnte man auch als konstantmarmoriert bezeichnen.

Sowohl die hetero- wie die homozygotmarmorierten Samen zeigen in ihrer Zeichnung eine recht beträchtliche Variation und scheinen auf Grund dieser häufig nicht sicher voneinander unterschieden werden zu

können. Wenn überhaupt ein Unterschied hervorgehoben werden soll, so wäre es der, dass die vom Hilum abgekehrte Samenhälfte bei den Homozygotmarmorierten häufig eine mehr oder weniger grosse Anzahl

Fig. 2. Drei Samen mit Heterozygotmarmorierung Mattmünzbronze/Veilchenartig Weiss. Hilumrand Bister.

rhomboidische Felder in der helleren Grundfarbe aufweist, die bei den Heterozygotmarmorierten nicht oder wenigstens seltener vorzukommen scheinen. Für die heterozygotmarmorierten Samen ist von mir (LAMPRECHT 1933) an einem grossen Material nachgewiesen worden, dass die dunkleren Flecken der Testa stets der durch einen Genotypus mit *CC* bedingten Testafarbe entsprechen, die des helleren Grundes einem im übrigen gleichen Genotypus mit *cc*. Hier ist die Farbenverteilung also in ihrer Abhängigkeit von der genotypischen Konstitution vollkommen bekannt. Wie die Farbenverteilung bei den homozygotmarmorierten Samen durch das Zusammenwirken von *M* mit den Farbgenen für die Testafarbe beeinflusst wird, darüber scheint bisher nichts sicheres bekannt zu sein. Aus oben Angeführtem geht klar hervor, dass die Heterozygotmarmorierung nur zweifarbig auftreten kann. Die homozygot-

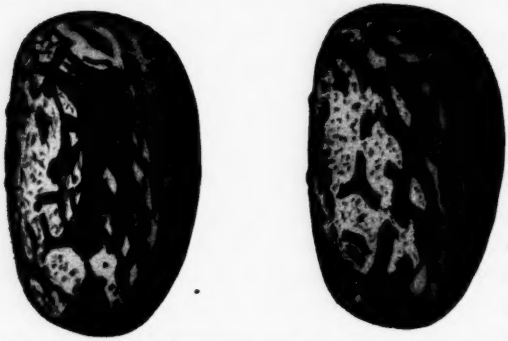

Fig. 3. Zwei homozygotmarmorierte Samen aus zwei verschiedenen reinen Linien. Linker aus L. 47, Huish Beauty, rechter aus L. 72, Early Prolific. Nur die Farbenverteilung, nicht die Form, ist genau wiedergegeben.

marmorierten Typen sind diesbezüglich kaum untersucht. Soweit mir bekannt, kommen hauptsächlich dreifarbige Kombinationen vor. Bevor in dieser Hinsicht Untersuchungen vorliegen erscheint es nicht ausgeschlossen, dass die Dreifarbigkeit auf eine Kombination von *M* und *S* zurückzuführen ist; wenigstens dürfte dies für solche Typen gelten bei denen die Zeichnung in den verschiedenen Farben wegen grosser Ähnlichkeit der letzteren schwer festgestellt werden kann. Gleichzeitig hetero- und homozygotmarmorierte Typen können durch Kreuzungen synthetisiert werden. Solche sind häufig vierfarbig und geben — mit Hinblick auf die Konstitution *Cc* — niemals konstante Nachkommen.

Der *gebänderte Typus* ist in Fig. 4 durch 3 Samen wiedergegeben. Der linke Same entspricht meiner Linie 9 aus der französischen Sorte

Fig. 4. Drei gebänderte (gestreifte) Samen. Linker aus Linie 9, Souvenir de Deuil, die beiden rechten aus Linie 145, »*Dolichos Zebra*» (siehe Text).

Souvenir de Deuil, die beiden rechten Samen der Linie 145 aus »*Dolichos Zebra*» (siehe weiter unten). Dieser Typus, der mir nur ein- und zweifarbig bekannt ist (einfarbig bei Bänderung auf weissem Grunde), wird dadurch charakterisiert, dass die Testa, seitlich betrachtet, auf hellerem Grunde eine, zwei oder mehrere Bänder (Streifen) in dunklerer Farbe aufweist, die fast stets Unregelmässigkeiten zeigen und bald hier, bald da unterbrochen, zum Teil in kleinere Flecken aufgelöst, bald miteinander mehr oder weniger verflossen sind. Wie aus Fig. 4 ersichtlich ist, verlaufen diese Bänder stets ziemlich deutlich gekrümmt konzentrisch um das Hilum. Diesen Typus habe ich u. a. mehrmals aus Botanischen Gärten unter der Bezeichnung *Dolichos Zebra* bzw. *Phaseolus Zebra* FINGERH. erhalten. Es handelt sich aber sicher nur um eine Form von *Phaseolus vulgaris*, denn teils zeigt diese Form in ihren

morphologischen Eigenschaften volle Übereinstimmung mit Rassen von *Ph. vulgaris*, teils kann sie mit diesen ohne weiteres gekreuzt werden und gibt hierbei fertile Nachkommen. Die Vererbung des gebänderten Typus ist u. a. von K. TJEBBES und H. N. KOOIMAN (1919, 1921) untersucht worden, die für diesen ein Genpaar *S—s* gefunden haben. Über die Farbenverteilung auf Bänderung und Grund, wie sie durch das Zusammenwirken von *S* mit den Farbgenen für die Testafarbe bedingt wird, scheint bisher nichts veröffentlicht zu sein. Durch Kreuzung können Kombinationen von Bänderung, Homo- und Heterozygotmarmorierung erhalten werden.

Den *gespritzten* Typus habe ich in der genetischen Literatur von *Ph. vulgaris* noch nicht erwähnt gefunden. Im Jahre 1928 fand ich als Beimengung in einer Partie Bohnen aus Ungarn drei Samen, die eine Kombination dieses Typus mit dem gebänderten darstellten. Es handelte sich offenbar um spontane Kreuzungen. Leider haben die aus diesen Samen erhaltenen Pflanzen infolge sehr später Reife hier in Schweden keine keimfähigen Samen gegeben. Später habe ich Samen vom gespritzten Typus unter der Bezeichnung *Ph. atropunctatus* aus Botanischen Gärten erhalten. Es handelt sich hier, gleichwie oben für *Ph. Zebra* erwähnt, um keine selbständige Art sondern sicher nur um eine Form von *Ph. vulgaris*, da teils volle Übereinstimmung in bezug auf die morphologischen Eigenschaften herrscht, teils bisher bei Kreuzung durchweg fertile Nachkommen erhalten wurden. Der Name *Ph. atropunctatus* kommt auch im Index Kewensis nicht vor und dürfte als Gartenbezeichnung aufzufassen sein. Das Aussehen des gespritzten Typus zeigt Fig. 5. Wie ersichtlich zeigt die Testa auf hellem Grunde eine Grossfleckigkeit in etwas dunklerer Farbe und überdies eine über das Ganze zerstreute dominierende Punktierung in dunkler Farbe. Letztere besteht aus Pünktchen verschiedener Grösse und ist gleichsam über die ganze Testa verspritzt.

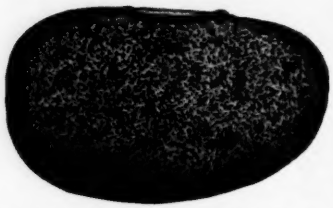

Fig. 5. Ein typisch gespritzter Same. Linie 53 aus *Phaseolus »atropunctatus»* (siehe Text).

2. *Teilfarbige Typen.* Bei diesen Typen ist, wie früher erwähnt, stets ein gewisser Teil der Testa reinweiss. Der gefärbte Teil der Testa hat seinen Ausgangspunkt stets vom Hilumrand. Samen bei denen die Umgebung des Hilums weiss, andere Teile aber gefärbt sind, scheint es nicht zu geben. Die farbigen Partien auf der Testa dieser Typen zeigen, abgesehen von kleineren Variationen in der Ausbreitung, stets eine sym-

metrische Anordnung zu beiden Seiten der Längsachse des Samens. Als Beispiel sind in Fig. 6 drei Samen vom *sellatus*-(= satteltragend)-Typus abgebildet. Bei den beiden linken Samen ist der farbige Teil Bister, beim rechten Samen dunkel Kastanienbraun. Diese drei Samen zeigen ungefähr die Variation dieses Typus. Zuweilen kommen noch ein oder zwei kleinere runde Flekken ausserhalb der Figur vor. In bezug auf weitere Typen verweise ich auf den späteren Teil der Arbeit. Bisher sind mir ungefähr 25 erblich verschiedene Typen von Teilfarbigen bekannt, von denen unten eine Anzahl beschrieben werden soll. Die Bezeichnung der Typen wird stets mit lateinischen Namen erfolgen, die auf die Form der farbigen Figur auf der Testa Bezug nehmen. Die weitere Einteilung der verschiedenen Typen von Teilfarbigen in Untergruppen kann in vollkommener Übereinstimmung mit jener erfolgen, die im Vorstehenden für die erste Hauptgruppe, die Ganzfarbigen, mitgeteilt worden ist, weshalb es genügen dürfte auf diese hinzuweisen.

Fig. 6. Drei Samen vom *sellatus*-Typus = Linie 10, 45 und 46, sowie ausgespalten in F_2 der Kreuzungen Nr. 27 und 34.

HISTORIK.

Im Jahre 1931 hat H. N. KOOIMAN eine Monographie über die Genetik von *Phaseolus* veröffentlicht, weshalb es vielleicht überflüssig erscheinen könnte, hier eine Übersicht über bisherige Resultate zu geben. Da indessen die genannte Monographie in mehreren Hinsichten sehr knapp und zum Teil unvollständig abgefasst ist sowie für mehrere Fälle eine kritische Diskussion der erhaltenen Resultate fehlt erscheint dies unerlässlich. Die unten mitgeteilten Werte für die theoretische Erwartung sowie für D/m sind vom Verfasser berechnet.

Die erste Mitteilung über die Vererbung der Teilfarbigkeit der Testa finden wir in einer Arbeit von EMERSON (1902). In dieser wird eine Anzahl von Kreuzungsresultaten ohne Angabe von Spaltungszahlen ganz allgemein besprochen. In einer Kreuzung zwischen einer teilfarbigen Sorte, Golden Wax, und einer ganzfarbigen, Mohawk, die

durch 5 Generationen studiert worden ist, konnte EMERSON zunächst feststellen, dass die Samen der F_1-Generation ganzfarbig waren. In der zweiten Generation trat eine Spaltung in ganzfarbige und teilfarbige Samen ein, und in den folgenden Generationen (siehe EMERSON, Pl. II) gaben die teilfarbigen Samen stets nur wiederum teilfarbige Nachkommen. In F_1 von zwei weiteren Kreuzungen, Keeney × Davis und Challenge Black × Wardwell (l. c. S. 40—41 und Pl. III), hatte EMERSON gleichfalls vollkommene Dominanz von Ganzfarbigkeit über Teilfarbigkeit feststellen können. Erwähnt sei, dass in dem einen von diesen zwei Fällen eine reinweisse Rasse, Davis, mit einer teilfarbigen, Keeney, gekreuzt worden ist, und auch hier sind die Samen der F_1-Generation ganzfarbig gewesen. Daraus kann geschlossen werden, dass in diesem Falle der Elter mit reinweisser Testa Träger der genotypischen Konstitution für Ganzfarbigkeit gewesen ist.

In einer späteren Arbeit berichtet EMERSON (1909) über analoge Kreuzungsergebnisse und veröffentlicht nun auch Spaltungszahlen. Auch hier wurden nach Kreuzung von ganzfarbigen mit teilfarbigen Rassen in F_1 stets nur ganzfarbige Samen erhalten. In F_2 von drei Kreuzungen wurde zusammen erhalten: 64 ganzfarbige : 30 teilfarbige und in F_3 von spaltenden ganzfarbigen Familien derselben Kreuzungen: 72 ganzfarbige : 25 teilfarbige. Bei Annahme einer monohybriden Spaltung wird im ersten Falle für D/m erhalten 1,55, im zweiten 0,18. Erwähnt sei, dass die Anzahl der Individuen für die einzelnen Kreuzungen zu klein ist um eine monohybride Spaltung sicher anzuzeigen; sie machen eine solche jedoch wahrscheinlich. Über die Verbreitung der Farbe bei den teilfarbigen Rassen wird nichts näheres mitgeteilt. EMERSON (l. c. S. 71) erwähnt nur, dass »the pigment usually appears around the »eye» of the seed, leaving the »back» without pigment. The pigmented area in »eyed» beans varies greatly in extent in different races and sometimes considerably within a race».

EMERSON (1909) teilt hier auch mit, dass in 7 Kreuzungen zwischen weisssamigen und teilfarbigen Rassen F_1 stets ganzfarbige Samen gezeigt hat. F_2 spaltet in Pflanzen mit ganzfarbigen, teilfarbigen und reinweissen Samen. In F_3 u. s. w. haben die geäugten Familien nie mehr ganzfarbige Nachkommen gegeben. Wohl aber haben gewisse eine Spaltung in Pflanzen mit geäugten und reinweissen Samen gezeigt. EMERSON erwähnt, dass in F_3 nach 7 Pflanzen das Spaltungsverhältnis 34 geäugte : 12 weisse erhalten worden ist. Andere geäugte gaben nur geäugte Nachkommen. Ganzfarbige gaben teils nur ganzfarbige, teils spalteten sie in ganzfarbige, geäugte und weisse, teils in ganzfarbige und

weisse und teils in ganzfarbige und geäugte. Weisssamige Individuen haben immer nur weisssamige Nachkommen gegeben.

Anschliessend hieran bespricht EMERSON die wahrscheinliche genotypische Grundlage für diese Spaltung, wobei er für Ganzfarbigkeit—Teilfarbigkeit das Genpaar *T*—*t* aufstellt. Zusammen mit dem Grundgen für die Ausbildung von Testafarbe *P* ergeben sich folgende Kombinationen:

P T — Ganzfarbig,
P t — Teilfarbig,
p T — Reinweiss (= ohne Pigment) mit Anlage zu Ganzfarbigkeit und
p t — Reinweiss mit Anlage zu Teilfarbigkeit.

Angesichts dieser vier möglichen Kombinationen sagt EMERSON voraus, dass in F_2 bzw. F_3 von Kreuzungen Reinweiss (*p*) × Teilfarbig Linien ausspalten sollen, denen die Konstitution *pt* zukommt. Dies hat EMERSON in einer späteren Arbeit (1911) nachweisen können, indem er nach Kreuzung verschiedener weisssamiger F_3-Familien mit Teilfarbigen in gewissen Fällen F_1-Individuen mit teilfarbigen Samen erhalten hat.

In seiner Arbeit von 1909 diskutiert EMERSON ferner die Möglichkeit, dass ausser den beiden oben angeführten Genpaaren *P*—*p* und *T*—*t* noch ein drittes, *E*—*e* (von eyed), Bedingung für die Ausbildung von teilfarbigen Typen sein könnte, ohne jedoch — wie er selbst betont — über Kreuzungsresultate zu verfügen, die dies bestätigen. Unter den vier möglichen Kombinationen mit *P* fasst EMERSON *Pte* als weissamig auf! Danach sollte also eine bifaktorielle Spaltung nach folgendem Schema möglich sein: 9 *PTE*, Ganzfarbig : 3 *PTe*, Ganzfarbig : 3 *PtE*, Teilfarbig : 1 *Pte*, Reinweiss. Es soll dies hier besonders hervorgehoben werden, da wir weiter unten Anlass haben werden darauf zurückzukommen. Ferner erwähnt EMERSON die Möglichkeit, dass die verschiedenen Typen von Teilfarbigkeit mit ungleicher Ausbreitung der Farbe durch besondere Faktoren, z. B. *E'*, *E''*, etc. bedingt sein könnten. Irgendeine Beschreibung oder Abbildung der untersuchten Typen von Teilfarbigen teilt EMERSON nicht mit.

E. v. TSCHERMAK (1912) widmete der Vererbung der »Äugung» an Rassen von *Ph. vulgaris* eine Untersuchung, in der er einleitend hervorhebt, dass die verschiedenen Formen von Verteilung des Pigmentes eine weitgehende Selbständigkeit in der Vererbung besitzen dürften. TSCHERMAK führte drei Kreuzungen mit derselben teilfarbigen Rasse,

»Runde geäugte» aus, die er folgendermassen (l. c. Fussnote S. 197) charakterisiert: »Die Pigmentierung betrifft die den Nabel einschliessende Längs- oder Bauchhälfte der Samenschale als kontinuierliches scharf abgegrenztes sog. Pigmentauge, welches von dem Strophiolum weiter hinauf gegen die Rückenkante reicht als in der anderen Querhälfte, welche die Mikropyle bzw. Radikula enthält». Auf Grund dieser Beschreibung und der von E. v. TSCHERMAK l. c. S. 208 wiedergegebenen Seitenansicht eines solchen Samens zu urteilen, handelt es sich hier sehr wahrscheinlich um den vorstehend in Fig. 6 abgebildeten *sellatus*-Typus.

Seine teilfarbige Rasse kreuzte E. v. TSCHERMAK mit zwei weisssamigen Rassen, 1) Weisse Wachs II und 2) Weisse Ilsenburger sowie mit einer ganzfarbigen, nämlich 3) Lange rotviolette Flageolet. F_1 ergab in allen drei Kreuzungen ganzfarbige Samen. F_2 bzw. F_3 und F_4 haben in diesen drei Kreuzungen folgende Spaltungen ergeben:

Kreuzung 1) F_2 : 47 Ganzfarbige : 10 Teilfarbige : 27 Reinweisse
D/m für
9 : 3 : 4 = 0,06 1,61 1,51

Kreuzung 2) F_2 : 19 Ganzfarbige : 1 Teilfarbige; D/m für 3 : 1 = 2,06
$F_3 + F_4$: 183 » : 57 » ; D/m für 3 : 1 = 0,45

Kreuzung 3) F_2 : 26 Ganzfarbige : 12 Teilfarbige : 13 Reinweisse
D/m für
9 : 3 : 4 = 0,76 0,88 0,08

Diese Spaltungen stehen offenbar in voller Übereinstimmung mit den schon von EMERSON gefundenen Resultaten, nämlich einer Spaltung nach 3 *T* : 1 *t* (Kreuzung 2) beziehungsweise kombiniert mit gleichzeitiger Spaltung in *P*—*p* (Kreuzung 1 und 3). E. v. TSCHERMAK ignoriert die von EMERSON (1909) eingeführte Genenbezeichnung *T*—*t* für Ganz- bzw. Teilfarbigkeit und verwendet hierfür anstatt dessen Z_1—z_1. Auch an Stelle von *P*—*p* (eingeführt von SHULL 1907) benutzt E. v. TSCHERMAK eine andere Bezeichnung, nämlich *A*—*a*.

Ausser den oben angeführten Spaltungen konstatierte E. v. TSCHERMAK eine Ausspaltung von drei verschiedenen Typen Teilfarbigen. Diese drei Typen sind von E. v. TSCHERMAK leider nur in skizzenmässigen Seitenansichten wiedergegeben, weshalb eine Identifikation des Typus mit geringer Farbenausbreitung um den Hilumrand nicht sicher erscheint. Sehr wahrscheinlich handelt es sich indessen um die drei Typen *sellatus*, »Piebald» (laut SURFACE 1916) und *virgarcus*, namentlich da analoge Spaltungen später von SURFACE (1916) und SAX &

McPHEE (1923) festgestellt worden sind. Der Piebald Typus ist hier in Fig. 7, der *virgarcus*-Typus in Fig. 8 wiedergegeben. Für die Spaltung mit Hinsicht auf die drei teilfarbigen Typen hat E. v. TSCHERMAK folgende Zahlen erhalten:

Kreuzung 1	$(F_2 + F_3)$: 13	*sellatus*	: 17	*Piebald*	: 11	*virgarcus*
» 2	$(F_3 + F_4)$: 11	»	: 26	»	: 12	»
» 3	(F_2) : 12	»	: 20	»	: 10	»
Zusammen:	36	*sellatus*	: 64	*Piebald*	: 33	*virgarcus*
Erwartet:	33,25	»	: 66,50	»	: 33,25	»
D/m für 1 : 2 : 1 =	0,55		0,26		0,05	

Wie ersichtlich stimmen die Resultate in allen drei Kreuzungen recht gut miteinander überein, weshalb ich es gewagt habe sie zu vereinigen. E. v. TSCHERMAK macht für diese, offenbar monohybride Spaltung ein Genpaar Z_2—z_2 verantwortlich. Ich behalte diese Bezeichnung bei, aber, da Z_1 mit T identisch ist, ohne die Indexzahl. Obenstehende Spaltung wäre demnach zu schreiben: 1 *tt ZZ* : 2 *tt Zz* : 1 *tt zz*.

Fig. 7. Drei Samen vom *Piebald*-Typus (laut M. SURFACE), ausgespalten in F_2 von Kreuzung Nr. 27 und 34.

KAJANUS (1914) erwähnt unter anderen Kreuzungsresultaten (Punkt 13) die Aufspaltung eines spontanen Bastardes mit der Sorte Métis (teilfarbig), nämlich: 32 Ganzfarbig : 10 verschieden Teilfarbig. Diese Spaltung kann offenbar nur als Bestätigung der von EMERSON und E.

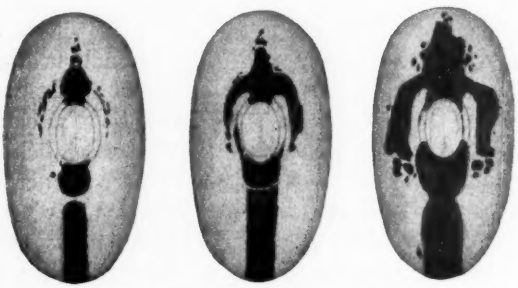

Fig. 8. Drei Samen vom *virgarcus*-Typus, den beiden Linien Nr. 36 aus Flageolet Victoria, und Nr. 57 aus Goldregen entsprechend. Man beachte den stark ausgebildeten Streifen, der über das Mikropylenende des Samens hinabreicht.

v. TSCHERMAK gefundenen Spaltung im Genpaar *T—t* aufgefasst werden.

Eine gute Vorstellung von der Variation des *sellatus*- und *virgarcus*-Typus bekommt man in einer von R. PEARL and F. M. SURFACE 1915 veröffentlichten Arbeit, in der diese Verfasser die Konstanz bzw. Variation der Teilfarbigkeit bei den beiden Sorten *Improved Yellow Eye* und *Old Fashioned Yellow Eye* studieren. Erstere Sorte gehört dem *sellatus*-Typus, letztere dem *virgarcus*-Typus an. L. c. sind in Fig. 40 32 Samen des ersteren, in Fig. 42 114 Samen des letzteren Typus abgebildet. Die dort wiedergegebene Variation stimmt gut mit der von mir an diesen beiden Typen gefundenen überein.

Kurz darauf berichtet F. M. SURFACE (1916) über die Spaltungsergebnisse nach Kreuzung der eben angeführten beiden Rassen. In der F_1-Generation wurden insgesamt 15 Pflanzen erhalten, die durchweg Samen vom »Piebald«-Typus (Fig. 7) trugen. Die Bezeichnung »Piebald« stammt von SURFACE, der l. c. sagt: »In the notes these F_1 beans have been designated »Piebald« because of the very irregular spotted pattern«. In der zweiten Generation spalteten die Nachkommen in gleicher Weise wie E. v. TSCHERMAK in seinen drei Kreuzungen konstatiert hat, nämlich nach dem Schema: 1 *sellatus* : 2 *Piebald* : 1 *virgarcus*. Hier ist es jedoch vollkommen sicher, dass es sich um den *virgarcus*-Typus handelt, da SURFACE klare Abbildungen der drei in Frage stehenden Typen veröffentlicht. Für diese Spaltung findet SURFACE in F_2, F_3 und späteren Generationen insgesamt folgende Zahlen:

Gefunden:	53	*sellatus* :	146	*Piebald* :	70	*virgarcus*
Erwartet:	67,25	» :	134,50	» :	67,25	»
D/m für 1 : 2 : 1 =	2,01		1,40		0,39	

In Übereinstimmung mit dieser monohybriden Spaltung nach dem *Zea*-Typus und mit schon von E. v. TSCHERMAK (1912) gefundenem konstatiert SURFACE, dass der Piebald-Typus eine Heterozygotform darstellt, die stets weiterspaltet. Wie ersichtlich wurden vom *sellatus*-Typus etwas weniger Individuen als erwartet erhalten. Gestützt hierauf macht SURFACE die Annahme, dass die hier vorliegende Spaltung dem Verhältnis 3 *sellatus* : 8 *Piebald* : 4 *virgarcus* entspräche, welches Verhältnis durch die gleichzeitige Spaltung eines Letalfaktors bedingt werden sollte, dessen Wirkung nur bei doppelthomozygoter Dosis und nur beim *sellatus*-Typus sich manifestieren sollte! Es dürfte wohl ohne weiteres selbstverständlich erscheinen, dass eine solche Annahme ohne weitere Beweise als unberechtigt zurückzuweisen ist. Denn trotz eines

gewissen Mangels an *sellatus*-Individuen sind die erhaltenen Spaltungszahlen doch fortwährend für die monohybride *Zea*-Spaltung als signifikativ aufzufassen. Schliesslich sei erwähnt, dass SURFACE für die in Rede stehende Spaltung ein Genpaar *I—i* verantwortlich macht, das also laut Vorstehendem mit *Z—z* zu identifizieren ist.

SHAW and NORTON (1918) berichten über die Spaltungsergebnisse in einer Reihe von Kreuzungen zwischen geäugten und ganzfarbigen bzw. reinweissen Typen. In 17 Kreuzungen zwischen ganzfarbigen und geäugten Typen fanden sie in F_2 und weiteren Generationen durchweg Spaltung nach dem Verhältnis 3 Ganzfarbig : 1 Teilfarbig. Zwischen geäugten und reinweissen Rassen wurden 6 Kreuzungen ausgeführt, die in F_2 und weiteren Generationen das Spaltungsverhältnis 9 Ganzfarbig : 3 Teilfarbig : 4 Reinweiss aufwiesen. Diese Ergebnisse bilden eine Bestätigung der schon von EMERSON gefundenen Resultate, nämlich Spaltung in den beiden Genpaaren *T—t* und *P—p*. SHAW and NORTON haben auch eine Spaltung in Typen mit verschieden grosser Äugung gefunden und machen hierfür zwei weitere Genpaare *R—r* und *S—s* verantwortlich. Da sie hierfür aber weder Zahlen noch anderes Tatsachenmaterial veröffentlichen, kann hierauf im weiteren nicht Rücksicht genommen werden.

K. SAX (1923) veröffentlichte die folgenden Resultate von drei Kreuzungen zwischen teilfarbigen und reinweissen Bohnenrassen. Kreuzung 1): Improved Yellow Eye 1310, also *sellatus*-Typus × Reinweiss 1333, F_2:

Gefunden:	201	Ganzfarbig :	68	Teilfarbig :	80	Reinweiss
Erwartet:	196,31	» :	65,44	» :	87,25	»
D/m für 9 : 3 : 4 =	0,50		0,35		0,90	

Diese Kreuzung bildet also eine Bestätigung des schon früher von mehreren Forschern konstatierten Spaltungstypus 9 *PT* : 3 *pT* : 4 *p*(*T* + *t*). Kreuzung 2) wurde ausgeführt zwischen einer teilfarbigen Rasse, Dot Eye, und Reinweiss 1228. Die teilfarbige

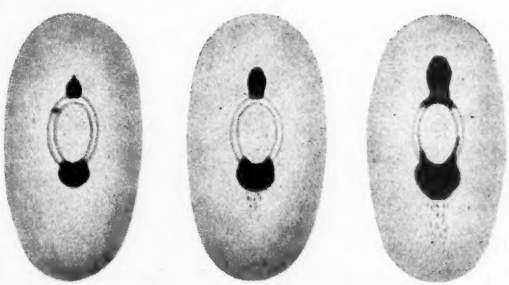

Fig. 9. Drei Samen vom *bipunctata*-Typus = Linie 5, sowie ausgespalten in F_2 der Kreuzung Nr. 32.

Rasse charakterisiert SAX folgendermassen: »The Dot Eye has only a very small pigmented area at either end of the hilum». Auf Grund dieser Beschreibung zu schliessen handelte es sich hier um die von mir als *bipunctata*-Typus bezeichnete Teilfarbigkeit. In Fig. 9 sind drei Samen dieses Typus abgebildet, die annähernd die Variation desselben angeben. SAX teilt keine Abbildungen mit. Seine Kreuzung 2) hat in F_2 folgendes ergeben:

Gefunden:	194	Ganzfarbig	: 28	Teilfarbig	: 67	Reinweiss
Erwartet:	203,20	»	: 13,55	»	: 72,25	»
D/m für 45 : 3 : 16 =	1,18		4,01		0,71	»

Wie ersichtlich sind hier zuviele Teilfarbige erhalten worden. Trotzdem dürfte es sich hier um eine Spaltung nach dem Verhältnisse 45 : 3 : 16 handeln, namentlich da SAX in seiner Kreuzung 3) eine analoge Spaltung mit guter Übereinstimmung der Zahlen mit den erwarteten erhalten hat. Vielleicht ist in Kreuzung 2) der Überschuss an Teilfarbigen auf eine Koppelung zurückzuführen. SAX' Kreuzung 3) wurde ausgeführt zwischen Improved Yellow Eye 1317, also *sellatus*-Typus, und Reinweiss 1228 und hat in F_2 folgende Spaltung ergeben:

Gefunden:	126	Ganzfarbig	: 12	Teilfarbig	: 41	Reinweiss
Erwartet:	125,86	»	: 8,39	»	: 44,75	»
D/m für 45 : 3 : 16 =	0,02		1,28		0,65	

Die Ergebnisse der beiden letzten Kreuzungen lassen es sicher erscheinen, dass die Teilfarbigkeit überhaupt nur bei Rezessivität in zwei Faktoren auftritt. Als Bezeichnung für das zweite hierfür verantwortliche Genpaar, also ausser *T—t*, können die von EMERSON (1909) für ein von ihm vermutetes solches Genpaar verwendeten Buchstaben *E—e* akzeptiert werden. Über eine eventuelle Aufspaltung in verschiedene Typen von Teilfarbigkeit erwähnt SAX leider nichts, und Abbildungen fehlen.

Im gleichen Jahre (1923) erschien eine Arbeit von K. SAX und MCPHEE, die über zwei Kreuzungen mit Teilfarbigen berichtet. Die eine Kreuzung ist offenbar identisch mit der früher von F. M. SURFACE (1916) ausgeführten, nämlich: Improved Yellow Eye (*sellatus*-Typus) × Old Fashioned Yellow Eye (*virgarcus*-Typus). F_1 zeigte den dort erwähnten Piebald-Typus, der auch hier in F_2 und folgenden Generationen im Verhältnisse 1 *sellatus* : 2 *Piebald* : 1 *virgarcus* spaltete. Insgesamt resultierten folgende Zahlen:

Gefunden:	386	*sellatus* :	805	*Piebald* :	402	*virgarcus*
Erwartet:	398,25	» :	796,50	» :	398,25	»
D/m für 1 : 2 : 1 =	0,71		0,43		0,22	

In bezug auf die teilfarbigen Typen besteht hier nicht der geringste Zweifel, da die Arbeit ein gutes Bild (Fig. 8) mit den Eltern-, F_1- und F_2-Samen enthält. Eine zweite von K. SAX u. MCPHEE erwähnte Kreuzung, ausgeführt zwischen Improved Yellow Eye und White 1333 spaltete in F_2 dem Verhältnis 9 Ganzfarbig : 3 Teilfarbig : 4 Reinweiss entsprechend. Es werden keine Zahlen mitgeteilt. Die Teilfarbigen spalteten in etwa 5 Typen. Eine Erklärung erschien auf Grund des geringen Materials unmöglich.

K. MIYAKE, Y. IMAI and K. TABUCHI (1930) veröffentlichten die Ergebnisse mehrerer Kreuzungen mit Teilfarbigen. Diese Verfasser erwähnen zuerst, dass Piebald gegenüber Ganzfarbig einfach rezessiv ist. Die Bezeichnung Piebald ist hier unglücklich gewählt, denn ihr Piebald-Typus hat gar nichts mit dem gleichnamigen und nur heterozygot vorkommenden Typus von F. M. SURFACE, K. SAX und MCPHEE zu tun. Er entspricht am ehesten dem Typus der bekannten Sorte Métis, den ich als *major*-Typus bezeichnen will. Fig. 10 zeigt drei Samen desselben. Bei Kreuzung dieses Typus mit Ganzfarbig war F_1 Ganzfarbig und F_2 spaltete in 3 Ganzfarbig : 1 *major*, also 3 *T* : 1 *t* entsprechend.

Fig. 10. Drei Samen vom *major*-Typus = Linie 6, der eine Elter der beiden Kreuzungen Nr. 25 und 33.

Eine zweite Kreuzung führten sie aus zwischen einem von ihren »Piebald»-Typen und einem anderen Typus mit geringerer Ausbreitung der Farbe, den sie als »saddle» bezeichnen. F_1 zeigte einen »Piebald»-Typus mit grösserer Ausbreitung der Farbe als ihr »Piebald»-Elterntypus. Für die Aufspaltung in der zweiten Generation teilen sie folgende Zahlen mit:

Gefunden:	261	»Bald» :	56	»Saddle» :	21	»Eye»
Erwartet:	253,5	» :	63,37	» :	21,13	»
D/m für 12 : 3 : 1 =	0,94		1,03		0,03	

MIYAKE, IMAI and TABUCHI bilden Samen der in F_2 ausspaltenden Typen ab, und zwar vier, die die Variation ihrer »Piebald»-Typen angeben, einen »Saddle»-Typus und 2 Varianten ihres »Eye»-Typus. Die vier abgebildeten »Piebald»-Typen gehören wahrscheinlich drei, aber wenigstens zwei verschiedenen erblichen Typen an. Leider lässt sich nichts sicheres hierüber aussagen, da diese Forscher nichts über die Frequenz der vier abgebildeten Varianten mitteilen. Ihre Bilder umfassen eine Variation, die der Gesamtvariation meiner drei Typen *major*, *minor* und *minimus* entspricht, die hier in den Figuren 10, 11 und 12 wiedergegeben sind. Ich habe Linien dieser drei Typen seit Jahren gebaut und ihre volle Konstanz in erblicher Hinsicht und damit Abgrenzung gegeneinander feststellen können. Aus den drei erwähnten Figuren geht jedoch auch hervor, dass jeder dieser Typen eine Variationsbreite in der Ausbreitung der Farbe bzw. des weissen Teiles aufweist, die in das Gebiet der Variation des nächsten Typus über-

Fig. 11. Drei Samen vom *minor*-Typus; aus Linie 65, Beurre nain Rapide und Linie 106 aus einer spontanen Kreuzung sowie ausgespalten in F_2 von Kreuzung Nr. 25.

Fig. 12. Drei Samen vom *minimus*-Typus = Linie 63, sowie ausgespalten in F_2 von Kreuzung 27 und 34.

Fig. 13. Drei Samen vom *sellatoides*-Typus, ausgespalten in F_2 von Kreuzung Nr. 25, 27 und 34.

greift. Daraus folgt, dass bei gleichzeitiger Ausspaltung dieser drei Typen in einer Kreuzung eine sichere Trennung derselben nur auf Grund von statistischer Bearbeitung mit Hinsicht auf den Grad der Ausbreitung der Farbe möglich sein wird.

Der zweite von MIYAKE, IMAI and TABUCHI abgebildete Typus »Saddle» ist nicht mit dem aus SURFACES Piebald-Typus ausspaltenden *sellatus*-Typus (satteltragend) identisch, sondern stimmt, auf Grund der Figur zu urteilen, am ehesten mit meinem *sellatoides*-Typus überein (siehe Fig. 13).

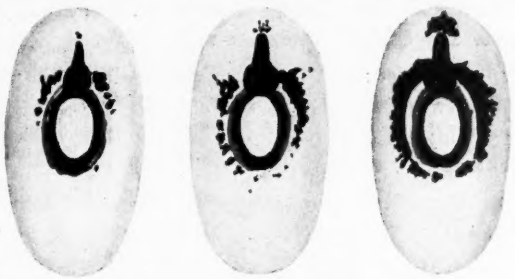

Fig. 14. Drei Samen vom *arcus*-Typus, ausgespalten in F_2 der Kreuzung Nr. 33.

Schliesslich finden wir l. c. zwei Varianten des »Eye»-Typus abgebildet, die gleichfalls sicher erblich verschieden sein dürften. Der linke Same entspricht mit ziemlicher Wahrscheinlichkeit meinem *arcus*-Typus, so benannt auf Grund des stets mehr oder weniger deutlichen Bogens (*arcus*) aussen um den Hilumrand, wenngleich sich dies auf Grund eines einzigen Samenbildes — also ganz ohne Kenntnis von Variation — nicht sicher feststellen lässt (siehe meine Fig. 14). Der zweite l. c. als »Eye»-Typus abgebildete Same entspricht wohl sicher meinem *laciniata*-Typus, so benannt auf Grund des von der Caruncula ausgehenden farbigen Zipfels (*laciniata* = zipfelig). Dieser ist hier in Fig. 15 abgebildet.

Fig. 15. Drei Samen vom *laciniata*-Typus, ausgespalten in F_2 der Kreuzung Nr. 33.

Mit Hinsicht auf das Angeführte dürfte es zweifellos erscheinen, dass in der in Rede stehenden Kreuzung nicht nur zwei sondern wenigstens drei Genpaare für Teilfarbigkeit an der Spaltung beteiligt sind. Ferner dürfte aus den Resultaten geschlossen werden können, dass

wenigstens einer der drei Typen *minimus*, *minor* und *major* über die Typen *sellatoides*, *arcus* und *laciniata* oder je eine derselben dominant ist.

In einer dritten Kreuzung, ausgeführt zwischen ihrem »Piebald»-Typus und einer ganzfarbigen marmorierten Rasse, fanden sie gleichfalls eine Spaltung in die oben erwähnten drei Typen, aber nun in einem anderen Verhältnis, nämlich:

Gefunden: 370 Ganzfarbig : 69 »Piebald» : 22 »Saddle» ; 31 »Eye».
Erwartet: 369,0 » : 69,19 » : 23,06 » : 30,75 »
D/m für
48 : 9 : 3 : 4 = 0,10 0,02 0,23 0,23

Das Verhältnis Ganzfarbige : Teilfarbige beträgt 370 *T* : 122 *t*, ist also klar monohybrid mit D/m = 0,10. Die Spaltung der Teilfarbigen scheint dem Verhältnis 9 : 3 : 4 zu entsprechen, kann jedoch mangels näherer Angaben über das Aussehen der Typen nicht diskutiert werden. Sowohl die Ganz- wie die Teilfarbigen spalteten überdies in Einfarbige und Homozygotmarmorierte. Hierfür wurden folgende Zahlen erhalten:

	Ganzfarbig Marmoriert		Ganzfarbig Einfarbig		Teilfarbig Marmoriert		Teilfarbig Einfarbig
Gefunden: 266		: 104		: 90		: 32	
Erwartet: 276,75	»	: 92,25	»	: 92,25	»	: 30,75	»
D/m für							
9:3:3:1 =	0,97		1,36		0,26		0,23

Hieraus kann geschlossen werden, dass die beiden Genpaare *M*—*m* und *T*—*t* (bzw. *E*—*e*) unabhängig voneinander vererbt werden.

Eine vierte Kreuzung haben MIYAKE, IMAI and TABUCHI ausgeführt zwischen einem bisher anscheinend nirgends erwähnten Typus von Teilfarbigkeit, den sie »Speckled» nennen, und einem einfachen, marmorierten »Piebald»-Typus. Ihren »Speckled»-Typus gebe ich in Fig. 16 wieder. Wie diese zeigt, hat dieser Typus sowohl die Grossfleckigkeit des SURFACEschen Piebald-Typus (aber andere Ausbreitung des farbigen Teils) sowie überdies über den weissen Teil der Testa zerstreute Pünktchen oder Tüpfelchen. Der von den genannten Verfassern verwendete zweite Elter

Fig. 16. Ein Same von *Speckled*-Typus laut M. MIYAKE, Y. IMAI und K. TABUCHI (1930) Plate II, Fig. 26.

wird l. c. in Fig. 16, Plate II wiedergegeben, und entspricht nach dieser zu urteilen dem *major*-Typus. F_1 zeigte den »Speckled»-Typus und F_2 spaltete im Verhältnis 244 Speckled : 85 einfach Piebald, also offenbar im monohybriden Verhältnis 3 : 1. D/m wird hierfür 0,35. Hervorgehoben zu werden verdient, dass hier bei dem »Speckled»-Typus die Grossfleckigkeit anscheinend als konstante, homozygote Eigenschaft aufzutreten scheint, während sie beim SURFACEschen Piebald-Typus nur für die Heterozygoten charakteristisch gewesen ist. Hier werden weitere Untersuchungen Klarheit schaffen müssen.

Eine fünfte Kreuzung schliesslich wurde ausgeführt zwischen Ganzfarbig—Einfarbig und Teilfarbig—Einfarbig (»Piebald»). F_1 war hier Ganzfarbig—Marmoriert, F_2 spaltete wie folgt:

Gefunden:	58	Ganzfarbig Marmoriert	: 64	Ganzfarbig Einfarbig	: 23	Teilfarbig Marmoriert	: 8	Teilfarbig Einfarbig
Erwartet:	57,38	»	57,38	»	19,12	»	19,12	»
D/m für 6:6:2:2 =	0,10		1,11		0,95		2,72	

Hier liegt offenbar eine Spaltung in *T*—*t* und *C*—*c* vor, wobei die marmorierten Typen durch *Cc* bedingt werden, demnach heterozygotmarmoriert sind. Die Spaltung wäre danach, laut obiger Reihenfolge, zu schreiben: 6 *T Cc* : 6 (*T CC* + *T cc*) : 2 *t Cc* : 2 (*t CC* + *t cc*). Über die Testafarben wird l. c. nichts Näheres mitgeteilt, weshalb keine Diskussion dieser Spaltung in bezug auf *C*—*c* möglich erscheint.

Wir wollen nun die oben besprochenen, bisher vorliegenden Resultate über die Vererbung der Teilfarbigkeit kurz zusammenfassen.

1. Ganzfarbigkeit dominiert vollkommen über Teilfarbigkeit; konstatiert von sämtlichen Verfassern.

2. Teilfarbigkeit manifestiert sich gleichwie Ganzfarbigkeit nur bei Anwesenheit des dominanten Grundgens für Testafarbe *P* (EMERSON 1909, 1911, E. v. TSCHERMAK 1912, SHAW and NORTON 1918, K. SAX 1923, SAX & MCPHEE 1923 sowie MIYAKE, IMAI and TABUCHI 1930).

3. Für die Spaltung Ganzfarbigkeit : Teilfarbigkeit wurde ein monohybrides Verhältnis, 3 : 1, von sämtlichen Verfassern gefunden. Hierfür wird das von EMERSON 1909 aufgestellte Genpaar *T*—*t* verantwortlich gemacht. Die von E. v. TSCHERMAK verwendete Bezeichnung Z_1—z_1 ist, als mit *T*—*t* höchst wahrscheinlich identisch, zu streichen.

4. K. SAX hat 1923 hierfür auch bifaktorielle Spaltung, dem Verhältnisse 15 Ganzfarbig : 1 Teilfarbig entsprechend, gefunden. Für das Auftreten von Teilfarbigkeit wären demnach zwei doppeltrezessive Gene

erforderlich. Für das zweite soll die Bezeichnung *E—e* benutzt werden, da EMERSON 1909 ein solches mögliches Genpaar diskutiert und so bezeichnet hat.

5. Die drei teilfarbigen Typen *sellatus, Piebald* und *virgarcus* werden durch ein Genpaar bedingt und zeigen demnach *Zea*-Spaltung. Dieses Genpaar soll mit *Z—z* bezeichnet werden, da E. v. TSCHERMAK 1912 wahrscheinlich diese Spaltung als erster konstatiert und das hierfür verantwortliche Genpaar mit Z_2—z_2 bezeichnet hat. Der Index wird weggelassen, da Z_1 als mit *T* identisch einzuziehen ist. Die Spaltung dieser drei Typen ist einwandfrei bestätigt und durch gute Abbildungen verifiziert von F. M. SURFACE 1916 und K. SAX u. MCPHEE 1923. Wir können daher schreiben:

sellatus-Typus *PP tt ee ZZ*
Piebald-Typus *PP tt ee Zz*
virgarcus-Typus *PP tt ee zz*

Dieser *Piebald*-Typus scheint demnach nur in heterozytoger Form vorzukommen.

6. F. M. SURFACE und K. SAX & MCPHEE haben die unter 5 erwähnte Spaltung nach Kreuzung von *sellatus* mit *virgarcus* erhalten, E. v. TSCHERMAK dagegen nach Kreuzung von Ganzfarbig bzw. Reinweiss mit *sellatus* (siehe vorstehend). Letzteres deutet darauf hin, dass die beiden Genpaare *T—t* und *E—e* als Grundgene für die Ausbildung von Teilfarbigkeit fungieren. Eine Unterscheidung der Wirkung dieser beiden Genpaare erscheint einstweilen unmöglich.

7. Die drei Typen von Teilfarbigen *minimus, minor* und *major* zeigen über die drei Typen *sellatoides, arcus* und *laciniata* bzw. je einen derselben wahrscheinlich Dominanz (M. MIYAKE u. a. 1930).

8. Der *Speckled*-Typus (Fig. 16) ist laut M. MIYAKE u. Mitarbeitern (1930) über den *major*-Typus dominant und diese beiden Typen zeigen monohybride Spaltung 3 : 1.

9. Die beiden Genpaare *M—m* (Homozygotmarmorierung) und *T—t* (bzw. *E—e*) scheinen unabhängig voneinander vererbt zu werden. Gleiches scheint auch für die beiden Genpaare *C—c* und *T—t* (bzw. *E—e*) zu gelten (M. MIYAKE, Y. IMAI and K. TABUCHI 1930).

EIGENE UNTERSUCHUNGEN.

Die erste hier zu besprechende Kreuzung, Nr. 32, wurde ausgeführt zwischen zwei reinen Linien, L 2 und L 5. L 2 stammt aus Neger, einer Wachsbohne, und hat ganzfarbige und reinschwarze Testa. Die

genotypische Konstitution für die Testafarbe dieser Linie ist *PP CC JJ gg BB VV,* was von mir früher (LAMPRECHT 1932a) nachgewiesen worden ist. Linie 5 stammt aus der französischen Brechbohnensorte Incomparable von VILMORIN-ANDRIEUX, Paris, und ist von mir seit 1929 mit jährlicher Auswahl neuer Pflanzen als Linie gebaut worden. Linie 5 ist teilfarbig und gehört dem in Fig. 9 dargestellten *bipunctata*-Typus an. Wie aus dieser ersichtlich zeigt dieser Typus nur zwei kleine, in ihrer Grösse allerdings variierende Flecken an der Stelle der Mikropyle und der Caruncula. Die häufigste Grösse der Flecken ist die am mittleren Samen in Fig. 9. Die in dieser Figur angegebene Variation wird nur selten überschritten, hierbei kann namentlich der farbige Fleck an der Caruncula noch etwas reduziert bzw. vergrössert, d. h. nach oben etwas verlängert werden. Ausser den beiden Flecken gewahrt man an Samen mit grösseren solchen eine Anzahl von äusserst feinen Pünktchen ausserhalb des Mikropylenfleckens in der Richtung gegen das Samenende zerstreut. Erwähnt soll werden, dass mir die Sorte Incomparable, von L. CLAUSE in Bretigny-sur-Orge, auch in einem anderen Typus von Teilfarbigkeit, *virgarcus*, bekannt ist.

Die beiden farbigen Flecken der L 5 sind homozygotmarmoriert, *MM*, und dreifarbig. Die Marmorierung ist Reinschwarz/Penséeviolett/Fliederartig Weiss. Das Penséeviolett entspricht im RC (= Répertoire de Couleurs publié par la Société des Chrysanthémistes et RENÉ OBERTHUR, 1905) Dunkles Stiefmütterchen-Violett, Pensée-Violett, 191/4 und noch dunkler bis fast Schwarz, im CS (= Color Standards and Color Nomenclature by ROBERT RIDGWAY, 1912) Dark Perilla Purple, XLIV, 69‴/k—l und dunkler (meistens) bis Dull Violet-Black, L, 61⁗m, in FT (= Farbentafeln nach OSTWALD) normal 10,5 pn, hell 9,5 pn, dunkel 11 pn bis fast schwarz und schliesslich im CC (= Code des Couleurs, KLINCKSIECK et VALETTE 1908) 585 und dunkler. Der helle Grund, Fliederartig Weiss entspricht RC 7/2—3 bis Veilchenartig Weiss (Violettfarbig Weiss) 6/2, CS Pale Vinaceous-Tawn, XL, 13‴ f bis Tilleul-Buff, XL, 17‴f. Diese Farbe dunkelt recht schnell nach und erreicht in der Regel schon nach einem Jahr etwa Vinaceous-Tawn, XL, 13‴ b. Ein sicheres Feststellen der drei Farben ist auch mit der Lupe gewöhnlich nur an Samen mit grösseren Flecken möglich.

In bezug auf die genotypische Konstitution für die Färbung der Testa unterscheidet sich Linie 5 also von Linie 2 im Gen für Homozygotmarmorierung *M* und ferner wenigstens in einem der beiden Gene für Teilfarbigkeit *T* und *E*. In einer noch nicht veröffentlichten Kreuzung ist ferner nachgewiesen worden, dass Linie 5 Träger des Farb-

TABELLE 1. *F_2 der Kreuzung Nr. 32: L 2 aus Neger × L 5 aus Incomparable. Die Aufspaltung in den beiden Genpaaren T—t und M—m.*

Nr.	Ganzfarbige		Teilfarbige		Summe Individuen
	Marmoriert Reinschwarz/ Penséeviolett /Fliederartig Weiss	Einfarbig Reinschwarz	Marmoriert Reinschwarz/ Penséeviolett /Fliederartig Weiss	Einfarbig Reinschwarz	
8501	19	8	6	4	37
8502	15	8	13	1	37
8503	24	7	3	1	35
8504	17	8	12	2	39
8505	17	2	5	3	27
8506	13	8	1	3	25
8507	13	8	2	3	26
8508	17	6	9	1	33
8509	19	8	3	1	31
8510	14	10	5	—	29
8511	22	3	5	3	33
8512	17	5	4	2	28
8513	29	7	7	5	48
8514	15	8	6	—	29
8515	16	5	6	1	28
8516	19	13	3	2	37
8517	21	7	3	4	35
8518	10	2	4	3	19
8519	17	11	6	3	37
8520	20	12	8	2	42
8521	18	6	14	2	40
8522	20	9	13	—	42
8523	19	5	10	1	35
8524	19	6	8	4	37
Summen:	430	172	156	51	809
Erwartet:	455,06	151,69	151,69	50,56	—
D/m für 9:3:3:1 =...	1,78	1,83	0,39	0,06	—

gens *R* ist. In bezug auf die übrigen 5 Farbgene *C, J, G, B* und *V* ist nichts bekannt.

Diese Kreuzung wurde 1930 ausgeführt, 1931 wurde F_1 und 1933 F_2 gebaut. Die auf F_1 erhaltenen Samen waren ganzfarbig marmoriert in den Farben Reinschwarz/Penséeviolett/Fliederartig Weiss. Die in

F_2 gefundene Spaltung ist in den Tabellen 1 und 2 dargestellt. Tabelle 1 zeigt die Spaltung ohne Rücksicht auf verschiedene Typen von Teilfarbigen. Wir finden zunächst die seit langem bekannte Spaltung

TABELLE 2. *F_2 der Kreuzung Nr. 32: L 2 aus Neger × L 5 aus Incomparable. Die Aufspaltung der Teilfarbigen in die verschiedenen Zeichnungstypen.*

Nr.	Zeichnungstypen der Teilfarbigen					Summe Individuen
	virgarcus stark	*virgarcus* schwach	*arcus*	*bi-punctata*	*virgata*	
8501	2	2	3	3	—	10
8502	3	5	5	1	—	14
8503	1	2	—	—	1	4
8504	5	3	4	2	—	14
8505	4	3	1	—	—	8
8506	1	2	1	—	—	4
8507	1	2	1	1	—	5
8508	3	3	1	2	1	10
8509	1	1	1	1	—	4
8510	—	2	1	1	1	5
8511	—	3	2	3	—	8
8512	2	2	—	2	—	6
8513	2	4	1	1	4	12
8514	1	2	2	—	1	6
8515	—	6	1	—	—	7
8516	—	3	1	—	1	5
8517	1	3	—	1	2	7
8518	1	3	—	3	—	7
8519	1	3	1	2	2	9
8520	2	7	—	—	1	10
8521	2	10	1	1	2	16
8522	—	8	—	5	—	13
8523	1	3	—	6	1	11
8524	1	6	—	3	2	12
Summen:	35	88	27	38	19	207
Erwartet für 3:6:3:3:1	38,81	77,63	38,81	38,81	12,94	—
D/m =	0,66	1,49	2,04	0,14	1,74	—

im Verhältnis $3\,T : 1\,t$, d. h. 602 Ganzfarbig : 207 Teilfarbig mit D/m = 0,39. Sowohl die Ganzfarbigen wie die Teilfarbigen spalten nur in zwei verschiedene Farbentypen, was von ganz besonderem Interesse sein dürfte. Wie ich in früheren Arbeiten gezeigt habe (LAMPRECHT 1932a, 1932b, 1933), spalten die fünf Farbgene *C, J, G, B* und *V* mit

grösster Wahrscheinlichkeit unabhängig voneinander. Linie 5 kann daher kaum in einem dieser fünf Gene von Linie 2 verschieden sein, denn solchenfalls müsste es zur Ausspaltung von anderen Farben kommen, was aber unter den 809 F_2-Individuen nicht der Fall gewesen ist. Ausserdem ist sicher festgestellt, dass Linie 5 Träger von *RR*, Linie 2 von *rr* ist. Wir können diesen beiden Linien demnach, unter der Voraussetzung dass der Unterschied Ganz—Teilfarbigkeit durch *T-t* bedingt wird, folgende Formeln zuschreiben:

Linie 2: *PP TT ee mm CC JJ gg BB VV rr*

Linie 5: *PP tt ee MM CC JJ gg BB VV RR*

Hiernach sollte eine Spaltung in drei Genpaaren stattfinden. Wie Tabelle 1 zeigt, wurde aber nur eine Spaltung in vier verschiedene Typen gefunden, für deren Erklärung die beiden Genpaare *T-t* und *M-M* genügen würden. Bei einer Spaltung in drei Genpaaren hätten wir, bei Voraussetzung dass die Heterozygoten sich nicht von den Dominanten unterscheiden, theoretisch acht verschiedene Typen zu erwarten, und zwar in folgender Frequenz: 27 *T M R* : 9 *T M r* : 9 *T m R* : 3 *T m r* : 9 *t M R* : 3 *t M r* : 3 *t m R* : 1 *t m r*. Erwähnt soll hierzu werden, dass die beiden Typen *TT mm CC JJ gg BB VV rr* und *TT mm CC JJ gg BB VV RR* Reinschwarz sind. Dies würde daher die Anzahl verschiedener Typen von acht auf sechs reduzieren. Bei einem Blick auf die oben für L 2 und L 5 mitgeteilten Formeln und auf die Spaltungsresultate in Tabelle 1 sehen wir ferner, dass wir anstatt vier verschiedenen marmorierten Typen nur zwei, und zwar mit den gleichen Farben erhalten haben. Es fehlen gerade die beiden infolge Umkombination zu erwartenden Typen *T M r* und *t M r*. Wenn wir eine so starke Koppelung zwischen *M* und *R* annehmen, dass hier in F_2 keine Umkombinationen auftreten, erhalten wir gerade das gefundene Verhältnis. Wir können dies folgendermassen schematisch zum Ausdruck bringen.

48 *T*
- 36 *M*
  - *R* Ganzfarbig Reinschwarz/Penséeviolett/Fliederartig
  - *r* 0 Individuen infolge starker Koppelung $\overset{\frown}{MR}$
- 12 *m*
  - *R* 0 » » » » $\overset{\frown}{mr}$
  - *r* Ganzfarbig Reinschwarz

16 *t*
- 12 *M*
  - *R* Teilfarbig Reinschwarz/Penséeviolett/Fliederartig
  - *r* 0 Individuen infolge starker Koppelung $\overset{\frown}{MR}$
- 4 *m*
  - *R* 0 » » » » $\overset{\frown}{mr}$
  - *r* Teilfarbig Reinschwarz

Wie ersichtlich resultiert bei Annahme einer solchen Koppelung gerade das gefundene bifaktorielle Spaltungsverhältnis 9 : 3 : 3 : 1. Diese Annahme ist einstweilen natürlich nur eine Arbeitshypothese und bedarf weiterer Bestätigung. Es könnte hier allerdings an noch eine Erklärungmöglichkeit gedacht werden, nämlich die, dass *MR* und *Mr* gleiche Phänotypen hervorrufen. Dann würden wir auch nur vier verschiedene Phänotypen finden. Diese Erklärung erscheint aber weniger wahrscheinlich.

Fig. 17. Drei Samen vom *virgarcus*-Typus mit schwach ausgebildeten Arcus und Streifen, ausgespalten in F_2 der Kreuzung Nr. 32.

Die gefundenen Spaltungszahlen sprechen mit grosser Wahrscheinlichkeit dafür, dass die beiden Genpaare *T—t* (bzw. *E—e*) und *M—m* unabhängig voneinander vererbt werden, bestätigen also in dieser Hinsicht, was M. MIYAKE, Y. IMAI and K. TABUCHI 1930 in einer kleineren Kreuzung gefunden haben.

Fig. 18. Drei Samen vom *virgarcus*-Typus mit gut ausgebildeten Arcus und Streifen, ausgespalten in F_2 der Kreuzung Nr. 32. Der Streifen ist gleichwie in Fig. 17 kurz, er reicht nicht um das Mikropylenende herum (vgl. den *virgarcus*-Typus in Fig. 8).

Tabelle 2 zeigt die Spaltung der Teilfarbigen in verschiedene Typen. Es konnten vier verschiedene Typen unterschieden werden und von einem von diesen überdies zwei Varianten. Wird auf diese beiden Varianten nicht Rücksicht genommen, so erhalten wir eine recht gute bifaktorielle Spaltung im Verhältnis 9 *virgarcus* : 3 *arcus* : 3 *bipunctata* : 1 *virgata*. Die beiden Varianten sind in Fig. 17 und 18 dargestellt. Aus diesen Bildern geht hervor, dass der *virgarcus*-Typus eine Kombination aus Elementen oder Teilen von drei verschiedenen Typen darstellt, diese sind *bipunctata* (Fig. 9), *arcus* (Fig. 14) und *virgata* (Fig. 19). Wir sehen

zuerst die beiden Flecken des *bipunctata*-Typus, je einen an der Mikropyle und an der Caruncula. Ferner sieht man den Bogen, dessen zwei Hälften am Carunculafleck entspringen und sich konzentrisch um das Hilum herabstrecken, wobei ein gewisser Abstand vom Hilumrand beibehalten wird. Hervorgehoben soll werden, dass der in Fig. 14 dargestellte *arcus*-Typus keine Kombination dieses Bogens mit dem *bipunctata*-Typus, sondern eine solche mit dem *laciniata*-Typus darstellt. Ferner sehen wir den Streifen, der beim *virgata*-Typus vom Mikropylenfleck gegen das Mikropylenende des Samens geht und schliesslich mehr oder weniger deutlich ausgebildet Punkte oder einen Fleck, gleichsam eine Verlängerung vom Carunculafleck gegen das Samenende dieser Seite bildend. Der letztere Teil der Zeichnung kommt bei dem in Fig. 19 dargestellten *virgata*-Typus nicht vor. Im Zusammenhang hiermit sei auch auf den *virgarcus*-Typus hingewiesen, der in Fig. 8 abgebildet ist. Bei diesem ist der vom Mikropylenfleck ausgehende Streifen bedeutend stärker ausgebildet und reicht stets um das Mikropylenende des Samens herum.

Fig. 19. Drei Samen vom *virgata*-Typus, ausgespalten in F_2 der Kreuzung Nr. 38.

Die beiden in Fig. 17 und 18 dargestellten Varianten des *virgarcus*-Typus unterscheiden sich vor allem in der verschieden starken Ausbildung des genannten Streifens und des *arcus*. Ob es sich wirklich um erbliche Unterschiede handelt erscheint noch nicht sicher, namentlich da es Übergänge gibt. Eine Aufteilung erschien indes insofern berechtigt, als die grosse Mehrzahl der Samen einer einzelnen Pflanze in der Regel entweder nur dem einen oder dem anderen Typus zugerechnet werden konnte.

Der *arcus*-Typus dieser Kreuzung entspricht nicht ganz dem in Fig. 14 wiedergegebenen aus Kreuzung Nr. 33. Erstens fehlt bei diesem in vorliegender Kreuzung der Zipfel des *laciniata*-Typus und ist hier durch den Fleck an der Caruncula ersetzt und zweitens kommt nicht selten eine Andeutung zu einem Streifen vom Fleck an der Mikropyle nach dem Samenende dieser Seite vor. Diese ist aber stets nur schwach, wie stark auch der Bogen zu sein scheint.

Beim *virgata*-Typus, der in Fig. 19 aus Kreuzung Nr. 38 abgebildet ist, kommt hier auch zuweilen eine schwache Andeutung des Bogens vom *arcus*-Typus vor. Sowohl der *arcus*- wie der *virgata*-Typus zeigen also in dieser Kreuzung eine modifikative Variation (an einer Pflanze vorkommend), derzufolge einzelne Samen als schwach ausgebildete *virgarcus*-Typus aufgefasst werden könnten. Beim *bipunctata*-Typus scheint dies dagegen niemals der Fall zu sein. Für den genotypischen Unterschied zwischen *virgarcus*- und *bipunctata*-Typus stelle ich das Genpaar *Bip—bip*, abgeleitet von der rezessiven Form *bipunctata*, auf. Mit Hinsicht auf ein zweites hier spaltendes Genpaar sollen zuerst die Ergebnisse weiterer Untersuchungen, vor allem in F_3, abgewartet werden. Erwähnt sei schliesslich, dass unter den Teilfarbigen eine Pflanze mit *virgata*-Samen aufgetreten ist, die von den übrigen stark dadurch abwich, dass die Samen auf der Caruncula-Seite nur einen kleinen Fleck (wie in Fig. 19, linker Same), auf der Mikropylenseite dagegen einen sehr starken und breiten Streifen zeigten, der über das Mikropylenende hinunterreichte.

Eine zweite Kreuzung, Nr. 38, wurde ausgeführt zwischen Linie 5 aus Incomparable und L 29 aus de la Chine. Der teilfarbige Elter, L 5, ist hier also der gleiche wie in der vorigen Kreuzung Nr. 32. Der zweite Elter, L 29, ist ganzfarbig und einfarbig, Geschwefeltes Weiss. Die Konstitution für die Testafarbe dieser Linie ist von mir früher (LAMPRECHT 1932 a) als *PP CC jj gg bb vv rr* nachgewiesen worden (auf *rr* ist auf Grund späterer Untersuchungen zu schliessen). Ausserdem muss diese Linie als ganzfarbig wenigstens eines der beiden Gene *T* und *E*, sowie als nicht marmoriert *mm* haben. Unter Hinweis auf die Diskussion über Linie 5 in voriger Kreuzung können wir für die beiden Eltern zu Kreuzung 38 schreiben:

Linie 5: *PP tt ee MM CC JJ gg BB VV RR*
Linie 29: *PP TT ee mm CC jj gg bb vv rr*

In bezug auf die Testafarbe finden wir hier also einen Unterschied in nicht weniger als vier Genen, was zur Ausbildung von etwa 16 verschiedenen Testafarben und bei Berücksichtigung von *M—m* zu etwa gleichviel marmorierten Typen Anlass geben sollte. Dies ist auch eingetroffen. Das Material der zweiten Generation dieser Kreuzung, 464 Individuen, ist jedoch zu gering, um eine Analyse der Spaltung in bezug auf Testafarbe zuzulassen. Es soll daher nur die Spaltung in Ganz- und Teilfarbigkeit sowie in verschiedene Typen dieser untersucht werden. Die Samen der ersten Generation waren ganzfarbig marmoriert.

In der zweiten Generation erfolgte nicht nur eine Spaltung in ganz- und teilfarbige Typen, sondern es spalteten auch Pflanzen mit rein-

TABELLE 3. *F_2 der Kreuzung Nr. 38: L 5 aus Incomparable × L 29 aus de la Chine. Die Aufspaltung in Ganzfarbige, verschieden Teilfarbige und Reinweiss.*

Nr.	Ganzfarbige	Teilfarbige				Reinweiss	Summe
		unipunctata	*bipunctata*	*virgata*	*virgareus*		
8568	8	2	1	—	—	1	12
8569	9	5	—	2	—	1	17
8570	7	—	—	—	—	4	11
8571	10	5	—	1	1	2	19
8572	15	6	—	1	1	—	23
8573	35	5	3	1	1	8	53
8574	8	2	—	—	—	2	12
8575	3	5	2	—	—	1	11
8576	12	—	—	—	—	—	12
8577	4	1	—	—	1	2	8
8578	12	3	—	3	—	2	20
8579	8	3	1	—	1	1	14
8580	8	—	—	—	1	—	9
8581	22	6	2	1	—	3	34
8582	16	3	—	—	—	3	22
8583	8	—	—	—	—	2	10
8584	8	1	—	—	2	2	13
8585	19	2	1	—	—	2	24
8586	4	1	—	1	1	3	10
8587	4	1	—	—	—	2	7
8588	7	3	—	1	—	1	12
8589	3	—	—	—	—	1	4
8590	12	1	2	—	—	3	18
8591	16	5	2	3	2	2	30
8592	7	1	—	—	1	1	10
8593	15	2	1	2	—	2	22
8594	9	2	1	—	—	2	14
8595	3	2	1	—	—	—	6
8596	4	1	—	—	—	2	7
Summen:	296	68	17	16	12	55	464

weissen Samen aus. Die erhaltenen Spaltungszahlen sind in Tabelle 3 wiedergegeben. Aus dieser Tabelle ergibt sich folgendes Spaltungsverhältnis:

296 Ganzfarbig : 113 Teilfarbig : 55 Reinweiss

Die Farbigen allein zeigen hier annähernd monohybride Spaltung im Verhältnis 3 : 1; D/m für 296 : 113 beträgt 1,28. Wie ist hier eine Ausspaltung von Pflanzen mit reinweissen Samen zu erklären? Früher ist von mir (LAMPRECHT 1932 a, 1932 c und 1933) nachgewiesen worden, dass reinweisse Samen genotypisch in zweierlei Weise bedingt werden können. Sämtliche Samen, die den Grundfaktor für Testafarbe in rezessiver Form haben, *p*, sind reinweiss und ferner alle Samen, die diesen Faktor in dominanter Form haben, *P*, die aber gleichzeitig alle Farbenfaktoren in rezessiver Form haben. In einer Kreuzung von zwei Linien mit farbigen Samen, die je nur Träger eines Farbenfaktors sind, soll es also in F_2 zur Ausspaltung von $^1/_{16}$ Pflanzen mit reinweissen Samen kommen, was von mir früher (1932 a) in Kreuzung Nr. 12 gefunden worden ist. Hier erscheint eine Ausspaltung von reinweissen Samen aus vorstehenden Gründen ausgeschlossen, da beide Eltern Träger eines und desselben Farbenfaktors sind. Aber auch wenn dies nicht der Fall wäre, so würde bei Heterozygotie in vier Farbenfaktoren nur mit einer Ausspaltung von $^1/_{256}$ Reinweissen zu rechnen sein, während hier etwa $^1/_8$ gefunden worden ist.

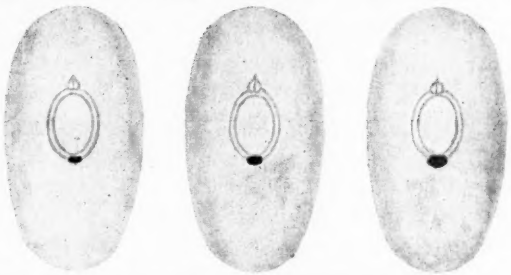

Fig. 20. Drei Samen vom *unipunctata*-Typus, ausgespalten in F_2 der Kreuzung Nr. 38.

An spontane Kreuzungen als Ursache kann nicht gedacht werden, denn erstens kommen solche in Schweden nur in einer Frequenz von etwa 0—3 Promille vor, zweitens würden dann nur gewisse Familien und nicht alle eine solche aufweisen können und drittens findet die Ausspaltung von Pflanzen mit reinweissen Samen in ganz regelmässiger Weise in der ganzen Kreuzung statt, d. h. in Familien mit grösserer Pflanzenanzahl kommt auch gewöhnlich eine entsprechend grössere Anzahl Pflanzen mit weissen Samen vor.

Es verbleibt da vorläufig wohl nur die Annahme, dass es eine oder gewisse Kombinationen von Genen für Teilfarbigkeit gibt, bei denen die ganze Testa ungefärbt verbleibt. Weitere Untersuchungen werden dies klarlegen.

Aus Tabelle 3 geht hervor, dass die Teilfarbigen in Kreuzung Nr. 38

in vier verschiedene Typen aufspalten. In grösster Anzahl kommt hier ein neuer, bisher nicht beschriebener Typus, *unipunctata* vor. Fig. 20 zeigt drei Samen dieses Typus. Wir sehen hier nur ein kleines farbiges Fleckchen an der Stelle der Mikropyle, das in seiner Grösse eine gewisse Variation aufweist. Es scheint niemals die Grösse des entsprechenden Fleckes beim *bipunctata*-Typus von L 5 zu erreichen. Meistens hat es nur die Grösse, wie sie am linken und mittleren Samen in der Fig. wiedergegeben ist. Bei diesem Typus ist es natürlich in den meisten Fällen unmöglich festzustellen, ob man es mit marmorierter oder gebänderter Testa zu tun hat.

In der Tabelle 3 sind ferner noch drei Typen von Teilfarbigen aufgenommen. Es ist überraschend hier feststellen zu können, dass diese von Kreuzung 32 bekannten Typen hier in geringerer Anzahl vorkommen als der *unipunctata*-Typus. Auch kommt der *virgarcus*-Typus, der in genannter Kreuzung klar über den *bipunctata*-Typus dominierte hier in geringerer, oder doch sicher nicht grösserer Anzahl, vor. Man bekommt den Eindruck, als ob sich hier die Wirkung eines Hemmungsfaktors geltend mache, der einen grösseren Teil eines oder mehrerer der übrigen Typen zu *unipunctata* reduziere.

In bezug auf die Typen sei ferner folgendes erwähnt. Unter den 17 Pflanzen mit *bipunctata*-Samen gab es vier, bei denen die beiden Flecken kleiner waren als beim üblichen Typus (Fig. 9 linker und mittlerer Samen); sie zeigten etwa die Grösse des Fleckchens beim *unipunctata*-Typus. Unter den *virgata*-Typen, 16 an der Zahl, gab es zwei mit sehr schwach angedeutetem Streifen auf der Mikropylenseite. Unter den 12 *virgarcus*-Typen gab es einen Samen mit sehr schwachem solchen Streifen und einen, bei dem der Bogen stark ausgebreitet war, etwa wie beim *diffusa*-Typus in Fig. 23 (aber ohne Lappen, siehe unten beim *lobata*-Typus). Es erscheint daher möglich, dass diese Kreuzung komplizierter ist als aus Tabelle 3 hervorgeht. Die dort mitgeteilten Zahlen deuten am ehesten auf eine bifaktorielle Spaltung. Sicher ist, dass durch die ganzfarbige Linie 29 eine ganz andere genotypische Konstitution für Teilfarbigkeit in die Kreuzung eingeführt worden ist als in der vorigen.

Eine weitere Kreuzung, Nr. 47, die nur in geringem Umfange ausgeführt worden ist, soll kurz angeführt werden, da in dieser das Verhältnis 15 Ganzfarbig : 1 Teilfarbig resultierte. Der eine Elter war Linie 44, aus Graue Spargel, mit ganz- und einfarbiger Testa in der Farbe Havannabraun, der andere war Linie 36, aus Flageolet Victoria, teilfarbig und marmoriert mit dem in Fig. 8 abgebildeten *virgarcus*-

Typus. F_1 hatte ganzfarbige, dunkelmarmorierte Samen. F_2 zeigte folgende Spaltung:

Gefunden:	177	Ganzfarbig : 20	Teilfarbig
Erwartet:	184,69	» : 12,31	»
D/m für 15 : 1 =	2,27.		

Der Wert für D/m ist gerade kein guter, aber sicherlich liegt doch eine bifaktorielle Spaltung vor. Für eine monohybride Spaltung wird D/m 4,82! Dies bestätigt zwei Kreuzungsresultate von K. SAX (1923), bei denen nach Kreuzung von Teilfarbigen mit reinweissen Rassen in F_2 eine Spaltung im Verhältnis 45 Ganzfarbig : 3 Teilfarbig : 16 Reinweiss erhalten worden ist. Wir können es demnach wohl als sicher betrachten, dass für Ausbildung der Teilfarbigkeit Rezessivität in zwei Genpaaren, *T—t* und *E—e*, erforderlich ist. Beide diese Gene dürften als Grundgene wirksam sein. EMERSONS (1909) Annahme, dass Samen der Konstitution *Pte* reinweiss sein sollten — die Annahme wurde ohne eine Stütze in Kreuzungsresultaten zu haben gemacht — steht hiermit im Widerspruch. Wäre sie richtig, so sollten in vorliegender Kreuzung Nr. 47 etwa $^1/_{16}$ Pflanzen mit reinweissen Samen erhalten werden. Solche fehlten indessen gänzlich.

Die Teilfarbigen zeigten in Kreuzung Nr. 47 folgende Spaltung:

10 *minor* : 6 *major* : 4 *virgarcus*

Die Zahlen sind zu klein um sichere Schlüsse zuzulassen. Vielleicht handelt es sich um eine Spaltung im Verhältnis 9 : 3 : 4. Sicher dürfte *virgarcus* gegenüber *minor* rezessiv sein.

Die nächste zu besprechende Kreuzung, Nr. 33, wurde ausgeführt zwischen Linie 6 aus Très nain précoce und Linie 29 aus de la Chine. L 29 wurde schon oben beschrieben. L 6 ist Teilfarbig und gehört dem in Fig. 10 abgebildeten *major*-Typus an. Die Testafarbe ist Rhamninbraun, hat demnach die genotypische Konstitution *PP cc JJ GG BB vv rr* für Testafarbe (siehe LAMPRECHT 1932 c). Unter Hinweis auf die Seite 203 für L 29 mitgeteilte genotypische Konstitution sowie die Teilfarbigkeit von L 6, kann den Samen der F_1-Generation folgende Konstitution zuerkannt werden: *PP Tt ee mm Cc Jj Gg Bb vv rr*. Die vier Farbgene *C*, *J*, *G* und *B* verursachen zusammen mit dem Grundgen für Testafarbe *P* die Farbe Mineralbraun und bei Heterozygotie in *C*: Heterozygotmarmoriert Mineralbraun/Rhamninbraun. Die auf F_1 erhaltenen Samen waren wie erwartet ganzfarbig und zeigten eben diese Farbe.

In F_2 haben wir auf Grund der mitgeteilten Formel mit Hinsicht

TABELLE 4. *F_2 der Kreuzung Nr. 33: L 6 aus Très nain précoce × L 29 aus de la Chine. Die Aufspaltung in Ganzfarbige, verschieden Teilfarbige und Reinweisse.*

Nr.	Ganzfarbige	Teilfarbige								Reinweisse	Summe
		bipunctata	*laciniata*	*arcus*	*virgarcus*	*virgata*	*lobata*	*diffusa*	*major*		
8525.....	4	1	2	—	—	—	1	—	1	2	11
8526.....	10	—	1	—	1	—	1	2	1	—	16
8527.....	19	1	—	—	—	—	—	—	—	—	20
8528.....	11	—	3	—	1	—	—	—	1	—	16
8529.....	4	—	1	—	—	—	—	1	—	—	6
8530.....	25	1	5	1	1	1	1	—	1	—	36
8531.....	25	2	3	—	2	—	—	—	—	3	35
8532.....	27	2	1	—	3	2	—	—	1	—	36
8533.....	43	1	2	4	2	—	1	1	—	1	55
8534.....	32	3	2	—	1	2	—	—	—	1	41
8535.....	20	2	—	3	1	—	—	—	—	—	26
8536.....	20	1	2	3	4	1	1	—	—	1	33
8537.....	33	2	2	2	2	—	—	3	—	1	45
8538.....	24	—	3	—	2	1	—	—	—	2	32
8539.....	20	1	2	2	—	1	—	1	1	—	28
8540.....	18	1	1	—	1	—	—	—	2	1	24
8541.....	42	6	2	—	1	1	—	1	—	2	55
8542.....	32	1	—	—	2	—	1	3	—	1	40
8543.....	7	—	2	3	2	1	—	—	—	—	15
8544.....	7	2	2	—	—	—	—	—	—	—	11
8545.....	5	—	1	—	1	1	—	1	—	1	10
8546.....	20	1	—	1	—	—	—	1	—	—	23
8547.....	13	2	2	2	1	1	—	3	1	—	25
8548.....	7	—	1	1	1	—	—	—	—	—	10
8549.....	9	—	—	1	—	—	—	2	1	—	13
8550.....	16	1	1	—	5	—	—	—	1	1	25
8551.....	13	3	3	1	2	—	—	2	1	2	27
8552.....	33	—	3	2	2	—	—	3	—	2	45
8553.....	11	1	1	1	1	—	—	—	—	—	15
8554.....	6	—	—	1	—	—	—	—	—	—	7
8555.....	10	2	—	—	1	—	—	2	—	—	15
8556.....	8	—	—	—	—	1	—	1	2	1	13
Summen:	574	37	48	28	40	13	6	27	14	22	809

auf die Testafarbe eine Aufspaltung in vier Faktoren zu erwarten, was, unter Hinweis auf früher Veröffentlichtes (LAMPRECHT 1933) zur Ausbildung von 15 verschiedenen einfarbigen und 8 verschieden hetero-

zygotmarmorierten Typen führen muss. Der in allen vier Farbgenen doppeltrezessive Typus wird Reinweiss sein; er soll demnach einmal unter 256 Individuen vorkommen. Unter den 809 Individuen der vorliegenden Kreuzung sind demnach etwa 3 mit reinweissen Samen zu erwarten. Von einer Mitteilung der Aufspaltung in Testafarben nehme ich Abstand, da die Individuenanzahl (809) zu gering ist um bei 24 verschiedenen Testafarben, und überdies verteilt auf Ganz- und Teilfarbige, einigermassen verwendbare Zahlen zu geben. Die Aufspaltung in Ganz- und Teilfarbige sowie Reinweisse ist in Tabelle 4 wiedergegeben. Diese zeigt hierfür folgende Spaltung:

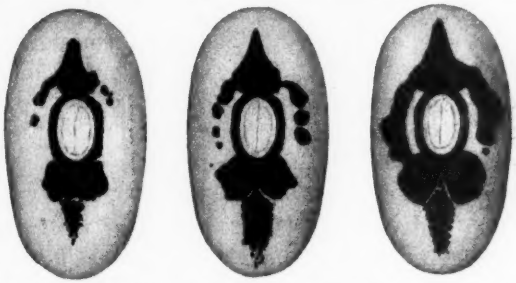

Fig. 21. Drei Samen vom *lobata*-Typus, ausgespalten in F_2 der Kreuzungen Nr. 25 und Nr. 33.

574 Ganzfarbig : 213 Teilfarbig : 22 Reinweiss

Das Verhältnis Ganzfarbig : Teilfarbig ist offenbar monohybrid, für 3 : 1 wird D/m = 1,35. Überraschend ist hier, gleichwie früher in Kreuzung Nr. 38, das Ausspalten von Reinweissen. In Kreuzung Nr. 38 war auf Grund der Konstitution der Testafarben überhaupt keine Ausspaltung von Reinweissen zu erwarten, in der vorliegenden Kreuzung sind jedoch, wie oben erwähnt, etwa 3 solche Individuen zu erwarten. Es kann als sicher betrachtet werden, dass die Ausspaltung des grössten Teiles der Reinweissen auf ähnliche Gründe zurückzuführen ist wie in Kreuzung Nr. 38, weshalb auf die dortige Diskussion verwiesen sei, namentlich da diese beiden Kreuzungen den gemeinsamen ganzfarbigen Elter, L 29, haben.

Fig. 22. Drei Samen vom *diffusa*-Typus, ausgespalten in F_2 von Kreuzung Nr. 33.

Wie aus Tabelle 4 hervorgeht, ist in dieser Kreuzung die Aufspaltung in verschiedene Typen von Teilfarbigen recht kompliziert, es sind nicht weniger als acht solche aufgenommen. Unter diesen kommen zwei neue, bisher nicht erwähnte Typen vor, nämlich der *lobata*- und der *diffusa*-Typus, abgebildet in Fig. 21 und 22. Am *lobata*-Typus lassen sich deutlich folgende Zeichnungselemente unterscheiden: der Zipfel des *laciniata*-Typus (Fig. 15), der Bogen des *arcus*-Typus (Fig. 14), der Streifen auf der Mikropylenseite des *virgata*-Typus (Fig. 19) und schliesslich zwei farbige Lappen von meistens charakteristischer Form, die vom Hilumrand an der Mikropyle entspringen und sich schräg nach aussen verbreiten. Auf Grund dieser letzteren hat dieser Typus seinen Namen erhalten: *lobata* = gelappt. Ob hier übrigens noch die Flecken oder der Punkt vom *bipunctata*- bzw. *unipunctata*-Typus vorhanden sind, lässt sich nicht entscheiden. Der in Fig. 22 abgebildete *diffusa*-Typus ist dem *lobata*-Typus in seinen Elementen sehr ähnlich, es hat den Anschein als ob die Wirkung eines weiteren Gens hinzugekommen wäre, das eine diffuse Ausbreitung der erwähnten Elemente bewirke. Dieses Gen scheint nach den Zahlen in der Tabelle zu urteilen dominante Wirkung zu haben.

Gleichwie in Kreuzung Nr. 38 finden wir auch hier eine Ausspaltung von *unipunctata*-Samen. Die genotypische Anlage für diesen Typus ist in beide Kreuzungen sehr wahrscheinlich durch den gemeinsamen Elter, L 29, eingeführt worden. In der zunächst zu besprechenden Kreuzung Nr. 25, die mit vorliegender L 6 als gemeinsamen Elter hat, sind keine *unipunctata*-Samen ausgespalten. Überblicken wir die bisher besprochenen Typen so wird immer deutlicher, dass diese aus verschiedenen Elementen zusammengesetzt werden, die wahrscheinlich je durch erbliche Anlagen bedingt werden, die ihrerseits eine Ausbreitung der Farbe von ganz bestimmten Zentren aus zu bewirken scheinen.

Eine nähere Diskussion der Spaltungszahlen soll erst erfolgen, wenn grösseres Material vorliegt.

Eine weitere Kreuzung, Nr. 25, wurde ausgeführt zwischen der zu voriger Kreuzung benutzten Linie 6 aus Très nain précoce und Linie 3 aus Leberfarbige. Linie 3 ist ganzfarbig und hat die Testafarbe Münzbronze, der die Formel *PP CC JJ gg BB vv rr* zukommt (LAMPRECHT 1932 a und 1933). Mit Hinblick auf die Ganz- und Einfarbigkeit dieser Linie und der Aufspaltung nach Kreuzung derselben mit einer Teilfarbigen im Verhältnisse $3\,T : 1\,t$, kann ihr die Formel *PP TT ee mm CC JJ gg BB vv rr* zugeschrieben werden. Unter Hinweis auf die früher für L 6 mitgeteilte Formel ist den Samen der F_1-Genera-

TAFEL I. 5. *F₁ der Kreuzung Nr. 25: L 3 aus Leberfarbige × L 6 aus Très nain précoce. Die Aufspaltung*

TABELLE 5. *F_2 der Kreuzung Nr. 25: L 3 aus Leberfarbige × L 6 aus Très nain précoce. Die Aufspaltung des Bastarden PP Cc JJ Gg BB vv Tt, Ganzfarbig Mineralbraun/Rhamninbraun marmoriert.*

Nr.	Ganzfarbige						Teilfarbige						Summe Individuen
	Mineralbraun	Mineralbraun/ Rhamninbraun marmoriert	Rhamninbraun	Münzbronze	Münzbronze/ Havannabraun marmoriert	Havannabraun	Mineralbraun	Mineralbraun/ Rhamninbraun marmoriert	Rhamninbraun	Münzbronze	Münzbronze/ Havannabraun marmoriert	Havannabraun	
8108	11	15	11	3	4	4	4	8	2	1	—	—	63
8109	2	17	6	6	5	1	2	4	2	1	2	1	49
8110	7	20	12	5	3	8	2	6	3	—	1	1	68
8111	15	17	8	4	9	3	1	2	2	—	—	—	61
8112	14	22	8	—	4	5	2	4	2	1	1	—	63
8113	4	16	9	2	6	1	4	2	2	—	1	1	48
8114	7	11	9	2	1	3	3	5	2	—	1	2	46
8115	9	22	5	7	4	5	4	3	2	1	3	1	66
8116	6	10	6	4	5	2	1	5	1	1	—	1	42
8117	6	23	7	3	5	2	1	6	2	1	1	1	58
8118	10	22	9	1	7	3	5	9	4	—	2	—	72
8119	8	15	8	3	7	2	1	6	3	2	3	—	58
8120	11	17	8	3	7	2	4	2	—	—	1	—	55
8121	9	13	7	1	6	1	4	2	2	3	2	—	50
8122	4	16	7	2	5	7	8	5	3	2	1	2	62
8123	10	18	7	3	6	4	3	4	1	1	1	1	59
8124	9	26	8	3	6	2	3	4	2	2	—	—	65
8125	10	14	10	2	10	5	4	8	1	1	1	1	67
8126	10	17	10	3	7	4	—	6	2	1	1	—	61
8127	6	15	9	3	5	6	4	9	1	2	1	—	61
8128	6	22	8	2	8	3	5	7	1	4	1	3	70
8129	3	12	9	4	5	2	—	8	3	2	1	1	50
8130	4	18	9	2	4	1	3	3	1	—	—	—	45
8131	8	20	8	5	5	3	1	4	5	2	2	—	63
Summen:	189	418	198	73	134	79	69	122	49	28	27	16	1402
Erwartet:	197,16	394,31	197,16	65,72	131,44	65,72	65,72	131,44	65,72	21,91	43,81	21,91	—
D/m für 9: 18:9:3:6:3: 3:6:3:1:2: 1	0,63	1,41	0,06	0,92	0,23	1,68	0,42	0,86	2,11	1,31	2,58	1,27	—

tion folgende Konstitution zuzuerkennen: *PP Tt ee mm Cc JJ Gg BB vv rr*. Sie sollen demnach Heterozygotmarmoriert Mineralbraun/Rhamninbraun sein, was auch gefunden worden ist. In F_2 haben wir demnach eine Aufspaltung in Ganz- und Teilfarbigkeit sowie in zwei Farbgenen (vier einfarbigen und zwei heterozygotmarmorierten Typen) zu erwarten.

Tabelle 5 zeigt die Spaltung in F_2 ohne Berücksichtigung der verschiedenen Typen von Teilfarbigkeit. In bezug auf die Spaltung in Teilfarbigkeit, *T—t*, und den beiden Farbgenen *C* und *G* ist kurz folgendes zu entnehmen: Für die Spaltung Ganzfarbigkeit : Teilfarbigkeit finden wir 1091 *T* : 311 *t*, also wahrscheinlich monohybride Spaltung nach 3 : 1; D/m ist hierfür 2,46. Für die beiden Genpaare *T—t* und *C—c* bzw. *G—g* resultieren folgende Zahlen:

Gefunden:	814 *TC*	: 277 *Tc*	: 246 *tC*	: 65 *tc*
Erwartet:	788,62 »	: 262,88 »	: 262,88 »	: 87,62 »
D/m für 9 : 3 : 3 : 1 =	+ 1,37	+ 0,97	— 1,15	— 2,51
Gefunden:	805 *TG*	: 286 *Tg*	: 240 *tG*	: 71 *tg*
Erwartet:	788,62 »	: 262,88 »	: 262,88 »	: 87,62 »
D/m für 9 : 3 : 3 : 1 =	+ 0,88	+ 1,58	— 1,57	— 1,84

Aus obigen Zahlen geht hervor, dass die in Frage stehenden Genpaare höchst wahrscheinlich unabhängig voneinander vererbt werden.

Über die Ausspaltung von verschiedenen Typen von Teilfarbigkeit in Kreuzung Nr. 25 gibt Tabelle 6 Aufschluss. Gleichwie in der vorigen Kreuzung Nr. 33 sind auch hier acht verschiedene Typen aufgenommen. Unter diesen kommen die beiden Typen mit der grössten Ausbreitung des farbigen Teils vor, nämlich *minimus* und *minor* (siehe Fig. 11 und 12). Erwähnt sei, dass beim *minor*- und *major*-Typus wie auch bei den übrigen Typen der mittlere Same in den Figuren den häufigsten Typus repräsentiert; eine Ausnahme hiervon bildet der *minimus*-Typus, indem bei diesem der linke Same den häufigsten Typus darstellt. Linien der drei Typen *minimus*, *minor* und *major* habe ich seit mehreren Jahren gebaut und ihre erbliche Verschiedenheit mit Sicherheit feststellen können. Um von der Variation des *minimus*-Typus eine Auffassung zu erhalten wurden die Samen von 17 Pflanzen, zusammen 1071, in Übereinstimmung mit der Ausbreitung der Farbe auf den drei in Fig. 12 abgebildeten Samen sortiert und gezählt. Resultat: 809 Samen entsprachen dem linken Samen, 222 dem mittleren und 40 dem rechten. Der Typus mit grösster Verbreitung der Testafarbe ist also der weitaus häufigste.

In bezug auf die Typen mit grosser Ausbreitung der Farbe, *minimus*, *minor*, *major*, sowie dem unten zu besprechenden *maximus* sei hervorgehoben, dass sie ohne und mit Fibula vorkommen können. Als Fibula bezeichne ich eine Aussparung der Testafarbe in der Nähe des

TABELLE 6. *F_2 der Kreuzung Nr. 25: L 3 aus Leberfarbige × L 6 aus Très nain précoce. Die Aufspaltung der Teilfarbigen in die verschiedenen Zeichnungstypen.*

Nr.	Zeichnungstypen der Teilfarbigen								Summe
	minimus	*minor*	*major*	*sellatoides*	*lobatus*	*virgarcus*	*virgata*	*bipunctata?*	
8108	1	4	—	4	—	4	2	—	15
8109	2	1	5	2	—	2	—	—	12
8110	2	2	2	2	—	2	3	—	13
8111	1	—	1	1	2	—	—	—	5
8112	—	4	—	1	1	1	3	—	10
8113	1	1	1	4	—	—	2	1	10
8114	3	1	3	3	2	1	—	—	13
8115	3	1	2	4	1	—	1	2	14
8116	1	—	3	2	2	—	1	—	9
8117	3	3	2	—	2	—	2	—	12
8118	3	3	1	5	4	1	3	—	20
8119	4	2	—	3	2	—	4	—	15
8120	—	1	3	1	1	—	—	1	7
8121	2	3	2	2	2	—	2	—	13
8122	3	2	2	4	1	2	5	2	21
8123	1	1	—	4	—	1	2	2	11
8124	1	—	2	4	—	2	2	—	11
8125	1	1	4	2	3	1	2	2	16
8126	1	3	2	1	1	—	2	—	10
8127	2	3	2	3	2	—	5	—	17
8128	2	2	5	6	2	1	2	1	21
8129	3	—	1	2	3	1	5	—	15
8130	2	—	1	1	—	—	3	—	7
8131	2	—	2	7	—	—	3	—	14
Summen:	44	38	46	68	31	19	54	11	311

Hilums in der Form von zwei bogenförmigen schmalen Streifen, die also einer Klammer (= Fibula) ähneln; siehe übrigens Fig. 23, die dies deutlich veranschaulicht. Der helle Streifen gleich unter dem Hilumrand in den beiden Figuren 10 und 12 stellt die Fibula in Seitenansicht dar. Die *minor*-Samen in Fig. 11 sind ohne Fibula abgebildet.

Aus Tabelle 6 geht hervor, dass in dieser Kreuzung ein neuer Typus.

maximus, ausgespaltet ist. Dieser steht dem *sellatoides*-Typus (Fig. 13) am nächsten, der wiederum dem *sellatus*-Typus (Fig. 6) am nächsten steht. Bei einem Vergleich des *maximus*-Typus (Fig. 24) mit den eben genannten beiden ergibt sich folgendes. Beim *sellatoides*-Typus hat sich die Farbe des *sellatus*-Typus in der Form von kleinen Fleckchen von der Caruncula über das diesseitige Ende des Samens herabverbreitet und gleichzeitig ist die gleichmässige Begrenzung des Sattels vom *sellatus*-Typus etwas unregelmässiger geworden. Beim *maximus*-Typus ist überdies noch der Streifen vom starken *virgarcus*-Typus hinzugekommen und vielleicht hat auch die Verbreitung der Farbe auf der Caruncula-Seite eine Ahnung zugenommen. Die übrigen in Tab. 6 aufgenommenen Typen sind bereits früher beschrieben. Dem *bipunctata*-Typus ist hier ein Fragezeichen beigegeben worden, da hier gewöhnlich eine schwache Andeutung zu einem Streifen auf der Mikropylenseite vorhanden war, weshalb es vor Untersuchung einer weiteren Generation nicht sicher erschien, ob es sich wirklich um diesen oder um eine Variante des *virgata*-Typus handelte. Schliesslich sei erwähnt, dass die beiden Typen *virgarcus* und *virgata* in je zwei Formen aufgetreten sind, nämlich teils mit dem Flecken vom *bipunctata*-Typus, teils mit dem Zipfel vom *laciniata*-Typus auf der Caruncula-seite.

Fig. 23. Ein Same vom *minimus*-Typus, ausgespalten in F_2 von Kreuzung Nr. 25, abgebildet von oben um die hier deutlich ausgebildete *Fibula* zu zeigen. Vgl. im übrigen Fig. 12.

Fig. 24. Drei Samen vom *maximus*-Typus, ausgespalten in F_2 von Kreuzung Nr. 33.

Auf eine Diskussion der Spaltungszahlen soll hier gleichwie in der vorigen Kreuzung wegen zu geringen Umfanges des Materials erst nach Erweiterung dieses eingegangen werden.

Die beiden letzten Kreuzungen, Nr. 27 und Nr. 34, die hier erwähnt werden sollen, können, da sie in bezug auf die hier in Frage stehenden Eigenschaften gleiche Spaltung aufweisen, gemeinsam behandelt werden. Diese beiden Kreuzungen haben den einen Elter, L 33 aus l'Inepuisable, gemeinsam. Dieser Linie kommt die Formel *pp TT ee*

mm cc JJ GG BB VV rr zu; in bezug auf die Farbgene, das Grundgen für Testafarbe sowie *M* siehe LAMPRECHT 1933, die Anwesenheit von nur einem der beiden Grundgene für Teilfarbigkeit in dominanter Form (*T* bzw. *E*) ergibt sich aus den folgenden Kreuzungsresultaten. Der zweite Elter in Kreuzung Nr. 27 war Linie 45, Teilfarbig vom *sellatus*-Typus mit Bister Testafarbe. Der zweite Elter in Kreuzung Nr. 34 war Linie 10, eine Geschwisterlinie zu L 45 mit gleichen Sameneigenschaften. Diesen beiden Linien ist also in bezug auf die Testafarbe folgende Formel zuzuerkennen: *PP tt ee mm CC JJ GG bb vv rr*. Die Samen der ersten Generation sollen also folgende Formel haben: *Pp Tt ee mm Cc JJ GG Bb Vv rr* und daher ganzfarbig, heterozygotmarmoriert Schwarz/Graulich Indigo sein. Die Resultate haben dies bestätigt.

In der zweiten Generation haben wir demnach, abgesehen von Aufspaltung in verschiedene Typen von Teilfarbigkeit, eine Spaltung in fünf verschiedenen Genpaaren, der Kombinationszahl 1024 entsprechend, zu erwarten. Die in den beiden Tabellen 7 und 8 hierfür mitgeteilten Zahlen zeigen, wie ersichtlich, mit der Erwartung durchweg befriedigende Übereinstimmung. Mit Hinsicht auf die den verschiedenen Testafarben zukommende Konstitution verweise ich auf Kreuzung Nr. 18 (LAMPRECHT 1933, S. 279—295), in der die gleichen Farben, aber ohne Teilfarbigkeit spalten. Im folgenden soll eine kurze Übersicht über die Spaltung der einzelnen Genpaare *P—p*, *C—c*, *B—b* und *V—v* zusammen mit *T—t* mitgeteilt werden.

Kreuzung Nr. 27.

Gefunden:	575 *TP*	: 173 *tP*	: 225 $(T+t)p$	
Erwartet:	547,31 »	: 182,44 »	: 243,25 »	»
D/m für				
9 : 3 : 4 =	+ 1,78	— 0,70	— 1,35	

Gefunden:	454 *TC*	: 121 *Tc*	: 133 *tC*	: 40 *tc*
Erwartet:	420,75 »	: 140,25 »	: 140,25 »	: 46,75 »
D/m für				
9 : 3 : 3 : 1 =	+ 2,56	— 1,80	+ 0,68	— 1,03

Gefunden:	440 *TB*	: 135 *Tc*	: 125 *tB*	: 48 *tc*
Erwartet:	420,75 »	: 140,25 »	: 140,24 »	: 46,75 »
D/m für				
9 : 3 : 3 : 1 =	+ 1,42	— 0,49	— 1,43	+ 0,19

TABELLE 7. *F_2 der Kreuzung Nr. 27: L 45 sellatus-Typus × L 33 m[illegible]lnepu*
Ganzfarbig Schwar[illegible]Graulic

Nr.	Ganzfar						
	Schwarz	Schwarz/ Graulich Indigo marmoriert	Kastanienbraun	Kastanienbraun/Ageratumblau marmoriert	Mineralbraun	Mineralbraun/ Rhamnin-braun marmoriert	Graul Indig
3661	9	11	1	2	2	7	4
3662	7	8	—	6	—	5	1
3663	4	1	2	2	1	1	3
3664	11	11	1	4	2	1	1
3665	6	19	6	5	4	5	6
3666	6	20	4	3	2	2	7
3667	3	3	1	1	1	—	3
8652	4	11	3	3	1	4	3
8653	7	15	3	2	1	3	5
8654	5	10	1	2	1	1	5
8655	2	9	—	—	—	—	—
8656	4	5	2	2	1	2	3
8657	8	17	1	12	—	4	4
8658	9	13	1	12	5	3	7
8659	8	22	4	6	3	4	9
Summen:	93	175	30	62	24	42	61
Erwartet:	76,97	153,93	25,66	51,31	25,66	51,31	76,
D/m für:	81 :	162 :	27 :	54 :	27 :	54 :	81
=	1,90	1,86	0,87	1,54	0,33	1,34	1,
	Teilfar						
3661	4	4	1	3	2	3	2
3662	1	—	—	1	2	—	—
3663	—	3	—	—	—	—	—
3664	1	5	—	1	2	1	2
3665	2	6	1	2	1	—	2
3666	—	2	1	1	2	1	2
3667	1	3	—	1	—	1	—
8652	2	3	1	2	—	1	1
8653	4	1	—	1	—	3	3
8654	3	2	—	2	—	1	1
8655	2	—	—	—	—	—	—
8656	1	2	1	—	—	—	—
8657	3	4	2	1	3	1	4
8658	5	8	—	1	—	—	—
8659	1	1	—	—	—	1	—
Summen:	30	44	7	16	12	13	17
Erwartet:	25,66	51,31	8,55	17,10	8,55	17,10	25
D/m für:	27 :	54 :	9 :	18 :	9 :	18 :	27
=	0,87	1,05	0,53	0,27	1,18	1,00	1,

L 33 ... Inepuisable. Die Aufspaltung des Bastarden Pp Cc JJ GG Bb Vv Tt, Schwarz Graulich Indigo marmoriert.

a n	f a r b i g e							
Mineralbraun/ Rhamninbraun marmoriert	Graulich Indigo	Bister	Bister/ Maisgelb marmoriert	Rhamninbraun	Ageratumblau	Maisgelb	Reinweiss	Summe
7	4	—	1	—	1	1	30	69
5	1	3	1	—	2	—	12	45
1	3	2	—	—	1	—	13	30
1	1	1	2	2	4	—	11	51
5	6	—	3	—	—	4	16	74
2	7	2	3	2	1	1	22	75
—	3	—	—	2	1	—	8	23
4	3	1	3	1	3	—	9	46
3	5	1	3	2	4	—	27	73
1	5	—	—	1	4	—	9	39
—	—	—	—	1	2	1	6	21
2	3	—	—	1	2	—	6	28
4	4	—	1	4	3	—	26	80
3	7	—	1	1	1	1	12	66
4	9	—	—	2	3	1	18	80
42	61	10	18	19	32	9	225	800
51,31	76,97	8,55	17,10	25,66	25,66	8,55	243,25	790,56
54 :	81 :	9 :	18 :	27 :	27 :	9 :	256	(832)
1,34	1,90	0,50	0,22	1,33	1,27	0,15	1,35	0,77
t e i l	f a r b i g e							
3	2	—	1	1	—	—	—	21
—	—	—	—	—	—	—	—	4
—	—	—	—	—	—	—	—	3
1	2	—	1	—	1	—	—	14
—	2	—	3	2	2	1	—	22
1	2	1	—	—	1	—	—	11
1	—	—	—	—	—	—	—	6
1	1	1	1	2	—	—	—	14
3	3	—	1	1	2	—	—	16
1	1	—	1	3	4	—	—	17
—	—	—	—	—	—	1	—	3
—	—	—	—	—	—	—	—	4
1	4	1	—	—	1	—	—	20
—	—	—	—	—	—	—	—	14
1	—	—	—	—	1	—	—	4
13	17	3	8	9	12	2	—	173
17,10	25,65	2,85	5,70	8,55	8,55	2,85	—	182,44
18 :	27 :	3 :	6 :	9 :	9 :	3 :	—	192
1,00	1,73	0,09	0,97	0,15	1,52	0,50	—	0,77

TABELLE 8. *F_2 der Kreuzung Nr. 34: L 10 sellatus-Typus × L 33 aus l'Inepuisable. Die Aufspaltung des Bastarden Pp Cc JJ GG Bb Vv Tt, Ganzfarbig Schwarz/Graulich Indigo marmoriert.*

Nr.	Ganzfarbige													
	Schwarz	Schwarz/Graulich Indigo marmoriert	Kastanienbraun	Kastanienbraun/Ageratumblau marmoriert	Mineralbraun	Mineralbraun/Rhamninbraun marmoriert	Graulich Indigo	Bister	Bister/Maisgelb marmoriert	Rhamninbraun	Ageratumblau	Maisgelb	Reinweiss	Summe
8558	9	13	1	2	1	5	2	—	1	—	1	—	12	47
8559	5	13	2	4	2	10	8	—	—	3	3	1	23	74
8560	7	22	3	6	2	4	5	—	6	5	3	—	29	92
8561	3	7	1	1	3	—	4	—	1	2	1	—	9	32
8562	7	11	1	4	2	2	9	1	2	2	1	—	25	67
8563	9	23	1	4	2	9	11	3	1	3	2	2	25	95
8564	9	11	1	2	—	6	5	2	—	—	2	1	14	53
8565	12	20	1	13	3	3	18	—	4	5	6	—	24	109
8566	7	27	1	4	10	7	13	2	2	3	8	—	34	118
8567	3	8	1	2	—	2	3	1	1	2	1	1	11	36
Summen:	71	155	13	42	25	48	78	9	18	25	28	5	206	723
Erwartet:	70,80	141,59	23,60	47,20	23,60	47,20	70,80	7,87	15,73	23,60	23,60	7,87	223,75	(727,19)
D/m für:	81:	162:	27:	54:	27:	54:	81:	9:	18:	27:	27:	9:	256	(832)
=	0,20	1,23	2,22	0,78	0,29	0,12	0,81	0,41	0,58	0,29	0,92	1,03	1,37	0,34
	Teilfarbige													
8558	2	1	—	—	—	1	1	1	—	—	—	—	—	6
8559	2	5	—	1	1	2	5	—	1	1	—	—	—	18
8560	1	6	2	3	—	1	6	—	1	1	1	—	—	22
8561	—	1	—	1	—	4	—	—	1	—	1	—	—	8
8562	1	8	1	—	1	1	4	1	—	1	—	1	—	19
8563	5	9	—	1	1	4	3	—	—	1	1	—	—	25
8564	3	2	1	1	2	2	5	—	—	—	2	—	—	18
8565	7	9	—	3	1	5	1	—	—	—	1	—	—	27
8566	5	9	—	1	1	4	3	—	—	—	1	—	—	24
8567	1	2	—	—	1	—	—	1	—	—	—	—	—	5
Summen:	27	52	4	11	8	24	28	3	3	4	7	1	—	172
Erwartet:	23,60	47,20	7,87	15,73	7,87	15,73	23,60	2,62	5,24	7,87	7,87	2,62	—	167,81
D/m für:	27:	54:	9:	18:	9:	18:	27:	3:	6:	9:	9:	3:	—	192
=	0,71	0,72	1,39	1,20	0,05	2,10	0,92	0,23	0,98	1,29	0,31	1,00	—	0,36

Gefunden:	453 *TV*	122 *Tv*	126 *tV*	47 *tv*
Erwartet:	420,75 »	140,25 »	140,25 »	46,75 »
D/m für				
9 : 3 : 3 : 1 =	+ 2,45	— 1,71	— 1,34	+ 0,04

Kreuzung Nr. 34.

Gefunden:	517 *TP*	172 *tP*	206 *(T + t)p*	
Erwartet:	503,44 »	167,81 »	223,75 »	»
D/m für				
9 : 3 : 4 =	+ 0,91	+ 0,36	— 1,37	

Gefunden:	381 *TC*	136 *Tc*	132 *tC*	40 *tc*
Erwartet:	387,56 »	129,19 »	129,19 »	43,06
D/m für				
9 : 3 : 3 : 1 =	— 0,50	+ 0,67	+ 0,27	— 0,48

Gefunden:	414 *TB*	103 *Tb*	143 *tB*	29 *tb*
Erwartet:	387,56 »	129,19 »	129,19 »	43,06 »
D/m für				
9 : 3 : 3 : 1 =	+ 2,03	— 2,56	+ 1,35	— 2,21

Gefunden:	387 *TV*	130 *Tv*	129 *tV*	43 *tv*
Erwartet:	387,56 »	129,19 »	129,19 »	43,06 »
D/m für				
9 : 3 : 3 : 1 =	— 0,04	+ 0,08	— 0,02	— 0,01

Bei einem Blick auf die oben mitgeteilten Zahlen kann man nur zu einem Schluss gelangen, dass nämlich die behandelten Genpaare mit grosser Wahrscheinlichkeit unabhängig voneinander vererbt werden. Die angeführten Zahlen berechtigen allerdings nur unter der Voraussetzung zu diesem Schluss, dass das Grundgen für Testafarbe nicht mit einem der in Rede stehenden Gene gekoppelt ist, denn solchenfalls würde ein Teil einer oder gewisser Kombinationen in den Weisssamigen verborgen bleiben. Dies ist aber sicherlich nicht der Fall. Dass *P—p* und die drei Farbgene unabhängig vererbt werden, geht aus mehreren früher veröffentlichten Untersuchungen hervor (LAMPRECHT 1932c und 1933), und auch *T* ist sicherlich nicht mit *P* gekoppelt, da das Genpaar *T—t* unter den farbigen Typen allein fehlerfreie monohybride Spaltung aufweist. Hierfür wurde in Kreuzung Nr. 27 erhalten: 575 *T* : 173 *t* mit D/m = 1,18 und in Kreuzung Nr. 34: 517 *T* : 172 *t* mit D/m = 0,02!

Die Teilfarbigen zeigten in diesen beiden Kreuzungen eine komplizierte Spaltung in wenigstens zwanzig verschiedene Typen, von denen

TABELLE 8. *F_2 der Kreuzung Nr. 34: L 10 selfatus-Typus × L 33 aus l'Inepuisable. Die Aufspaltung des*

eine Reihe auch bereits in F_3 untersucht worden sind. Die Veröffentlichung dieser Resultate soll, nach weiterer Komplettierung, einer künftigen Arbeit vorbehalten bleiben.

SUMMARY.

1. In the introduction the author gives a survey of the distribution of the colours of the seed coat in *Phaseolus vulgaris* and arrives at the following grouping: 1. Wholly coloured, 2. partly coloured; each of these two groups being sub-divided into a) unicoloured, b) multicoloured. The latter group is divided into: marbled (homozygously and heterozygously marbled or constantly and inconstantly marbled), streaked and sprinkled (a new type). In all groups there can occur caruncula stripe, corona, margo and micropyle streak.

2. In the historical review the author then gives a critical analysis of the results hitherto published in the literature with regard to the hereditary transmission of partial coloration, and in this connexion gives an account of the results obtained in seven crosses made by himself between different types of partly coloured and wholly coloured or pure white races. On the basis of these results and those of earlier investigations the author draws the following conclusions.

3. The formation of partly coloured seed coats takes place only if the two fundamental genes *T* and *E* are present in a double recessive dose: *tt ee*. With *T* or *E* the seed coat will be wholly coloured. As far as their effect is concerned it has not been possible so far to differentiate these two genes.

4. In the present work in all 17 hereditarily different types of partial coloration have been described and reproduced. In conformity with their coloration these various types, with the exception of those already denominated, have been given the following designations: *arcus, bipunctata, diffusa, laciniata, lobata, major, maximus, minor, Piebald, sellatoides, sellatus, Speckled, unipunctata, virgarcus* (two variations) and *virgata*.

5. In addition to the types included here the author is acquainted with several others not yet published so that the entire number of partly coloured types certainly amounts to at least 22, caused by at least four, probably five, different pairs of genes.

6. Two of these pairs of genes have been designated *Z—z* and *Bip—bip* respectively. *Z—z* is the foundation of the segregation 1

sellatus (*ZZ*) : 2 *Piebald* (*Zz*) : 1 *virgarcus* (*zz*). *Bip—bip* is the basis of the segregation 3 *virgarcus* (*Bip*) : 1 *bipunctata* (*bip*).

7. The investigation appears to produce clear evidence that the different types of partial coloration are composed of parts, each one corresponding to a definite hereditary material. Hence, these cause the distribution of the colour from various centres in the seed coat. The figures will clearly show this phenomenon.

8. A specially interesting observation made is that in two of the crossings performed between wholly coloured and partly coloured races a segregation of a noteworthy number of white-seeded plants has taken place, when such a segregation, in view of the genotypic constitution of the seed coat colour, was not expected at all in one case or only in very small numbers in the other. The author presumes that a certain combination of genes of partial coloration or an arresting gene has prevented the formation of seed coat colour.

9. In connexion with the fundamental factor for partial coloration, *T—t* (or *E—e*), the inheritance of the following pairs of genes has been examined: *P—p, M—m, C—c, G—g, B—b* and *V—v*. All these, together with *T—t,* have shown free combination (irrespective of inheritance). Whether the dominating factor in the individual cases was *T—t* or *E—e* could not be definitely determined.

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BEITRÄGE ZUR KENNTNIS DER ZYTOLOGIE DER RUBIACEEN

VON *FOLKE FAGERLIND*

STOCKHOLM

(Vorläufige Mitteilung)

DIE zytologischen Verhältnisse der Familie *Rubiaceae* sind bisher wenig bekannt. Die ersten Chromosomenzahlen sind in der embryologischen Abhandlung von LLOYD (1902) mitgeteilt worden. LLOYD gibt die Zahlen für *Asperula montana* (n = 12) und für zwei Arten der Gattung *Crucianella* (n = 10) an. Die Zahl von *Coffea* wurde zu n = 8 (VON FABER 1912), die von *Houstonia* zu n = 16 (STEVENS 1912) und die von zwei *Oldenlandia*-Arten zu n = 9 bzw. 18 (HAGERUP 1932) bestimmt. In einer kleinen »vorläufigen Mitteilung» teilt HOMEYER (1932) eine ganze Reihe Zahlen, hauptsächlich für die Rubiaceen-Gruppe *Stellatae* mit. Weder die Angaben LLOYDS noch die VON FABERS konnten von mir bestätigt werden und dasselbe gilt für die Zahl HOMEYERS, n = 11, für *Phuopsis stylosa*.

Seit einigen Jahren bin ich mit einer Untersuchung der zytologischen und embryologischen Verhältnisse der Familie *Rubiaceae* und vor allem der Gruppe *Stellatae* beschäftigt. Als Resultat hat die zytologische Seite der Untersuchung unter anderem einige interessante Chromosomenzahlen geliefert. Die untenstehende Tabelle enthält die Zahlen, die von mir als korrekt betrachtet werden. Die Initialen H und F nach den Zahlen geben an, ob HOMEYER oder ich die Zahlenbestimmungen gemacht hat, H & F, dass HOMEYER und ich voneinander unabhängig die Zahlen gefunden haben. Nur die 2n-Zahl wird angegeben, auch wenn die n-Zahl gezählt worden ist.

Coffea arabica L.	22 H
» »	44 F
» *semiexcerta* COLEBR.	22 H
Pentas carnea BENTH.	20 F
Phyllis nobla L.	22 F
Spermacoce tenuior GÆRTN.	28 F
Gardenia florida L.	22 F
Psychotria undulata MIQ.	22 F

Bouvardia corymbosa Humboldti 36 F
» *hybrida* 36 F
Oldenlandia capensis L. 18 HAGERUP
» *senegalensis* HIERN. 36 »
Houstonia coerulea L. 16 STEVENS

Sherardia L.

arvensis L. 22 H & F

Crucianella L.

maritima L. 22 H
glauca var. *gilanica* K. SCH. 22 H
latifolia L. 44 H & F
Sintenisii 22 H
imbricata BOISS. 22 F
angustifolia L. 22 F
graeca BOISS. 22 F
aegyptiaca L. 22 F
chlorostachys FISCH. 22 H & F

Phuopsis GRIS.

stylosa GRIS. 20 F

Asperula L.

molluginoides REICHB. 20 F
azurea JOUB. & SPACH. 22 F
setosa » » » 22 F
montana WILLD. 22 H
Neilreichii RECK. 22 F
cynanchica L. 44 H & F
aristata L. 44 F
hirta RAMUND. 22 F
nitida S. S. 44 H & F
hexaphylla ALL. 44 H
tinctoria L. 44 F
ciliata ROCH. 44 F
asperrima BOISS. 22 F
glauca (L.) BESS. 44 F
taurina L. 22 H & F
odorata L. 44 H

Galium L.

Mollugo L. 22 H & F; 44 H & F; 45 F; 66 F
tyrolense W. 44 F
polonicum BLOCKI 44 H & F
ochroleucum WOLFN. 44 H & F
laevigatum L. 44 F
Schultesii VEST. 66 F
lucidum ALL. 22 H & F; 44 H
sp. aus Arkadien 22 F
verum L. 22 F; 44 H & F; 66 F
ruthenicum WILLD. 44 F
firmum TSCH. 22 H
flavescens BORB. 22 H
purpureum L. 22 F
saxatile L. 44 F
pumilum var. *balatonica* BARB. 44 H
anisophyllum VILL. 44 F
helveticum WEIGEL. 66 H
trifidum L. 24 F
palustre L. 24 F; 96? (95) F
uliginosum L. 22 H; 44 F
boreale L. 44 F; 66 H
physocarpum LEDEB. 66 F
rubioides L. 132? (134) F
Cruciata (L.) SCAP. 22 F
vernum SCAP. 44 F
articulatum ROEM. 22 F

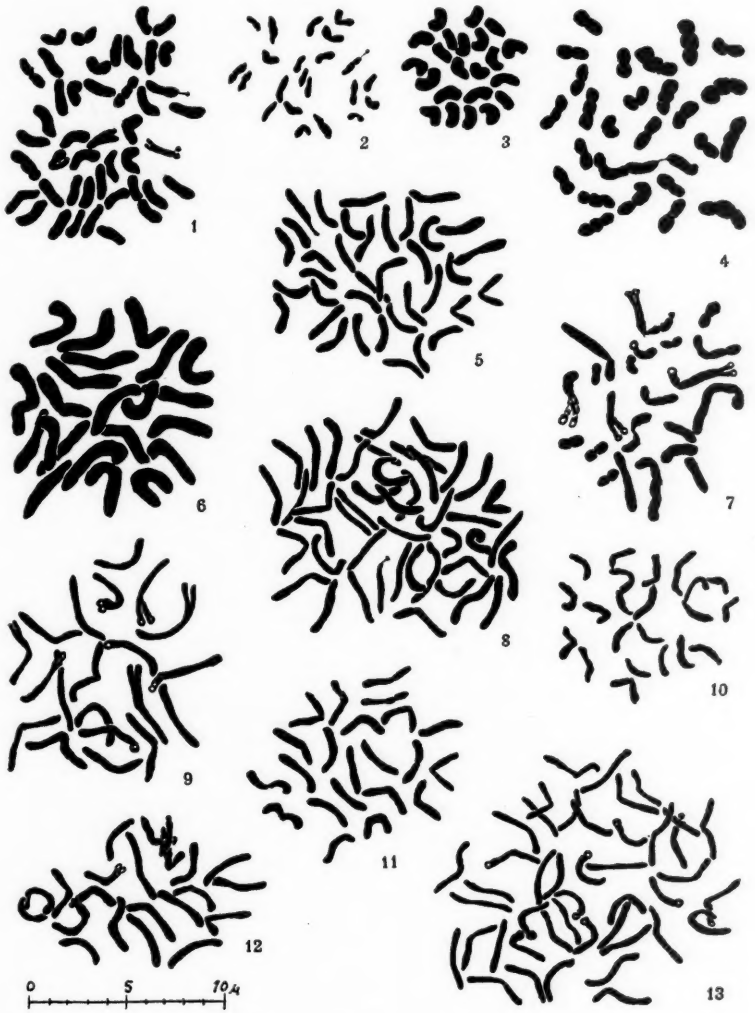

Fig. 1. *Coffea arabica.* — Fig. 2. *Phyllis nobla.* — Fig. 3. *Gardenia florida.* — Fig. 4. *Spermacoce tenuior.* — Fig. 5. *Bouvardia corymbosa Humboldtii.* — Fig. 6. *Psychotria undulata.* — Fig. 7. *Crucianella aegyptiaca.* — Fig. 8. *Asperula tinctoria.* — Fig. 9. *A. molluginoides.* — Fig. 10. *A. setosa.* — Fig. 11. *A. azurea.* — Fig. 12. *A. Neilreichii.* — Fig. 13. *A. nitida.*

saccharatum ALL.	22 H & F	*parisiense* var. *trichocarpum* TSCH.	66 F
Vaillantii DC.	20 F	*verticillatum* DANTH.	22 F
spurium L.	20 F	*murale* (L.) ALL.	44 F
sp. vom Richthofengebirge	44 F	*graecum* L.	22 F
aparine L.	66? (64) F 88? (86) F	*setaceum* LAM.	22 F 44 F
parisiense L.	22 F 44 H & F 66 F	*cassium* BOISS.	22 F

Mericarpaea BOISS.

Vaillantoides BOISS. 22 F

Vaillantia TOURN.

hispida L.	18 F	*muralis* L.	18 F

Rubia L.

cordifolia HOCHST.	22 F	*Olivieri* RICH	44 F
tinctoria L.	44 F	*chilensis* MOL.	22 H
» var. *iberica*	44 H	*peregrina* L.	132? (135) F

Callipeltis STEV.

cucullaria STEV. 22 F

Die *Stellata*-Rubiaceen werden also durch die Grundzahlen 9, 10, 11 und 12 und durch eine ausgeprägte Polyploidie charakterisiert. Diploide, tetraploide, hexaploide, octoploide und dodecaploide Arten sind repräsentiert.

Beim Studium der obenstehenden Chromosomenliste wird das Interesse auf einige Arten gelenkt, für die mehr als eine Chromosomenzahl angegeben worden ist, nämlich

1.	*Galium*	*setaceum*	mit	den	Zahlen	22 und 44
2.	»	*parisiense*	»	»	»	22, 44 und 66
3.	»	*aparine*	»	»	»	66 und 88
4.	»	*boreale*	»	»	»	44 und 66
5.	»	*uliginosum*	»	»	»	22 und 44
6.	»	*palustre*	»	»	»	24 und 96
7.	»	*verum*	»	»	»	22, 44 und 66
8.	»	*lucidum*	»	»	»	22 und 44
9.	»	*Mollugo*	»	»	»	22, 44 und 66

Es gibt also nicht weniger als neun *Galium*-Arten, von denen jede durch Typen repräsentiert ist, die eine polyploide Serie bilden. Die Zahlen für *G. Mollugo* sind sowohl in somatischen Zellen (Wurzel-

spitzen) als auch durch das Studium der Reduktionsteilung bestimmt worden. Zufolge der Schwierigkeit eine octoploide Art direkt aus einer

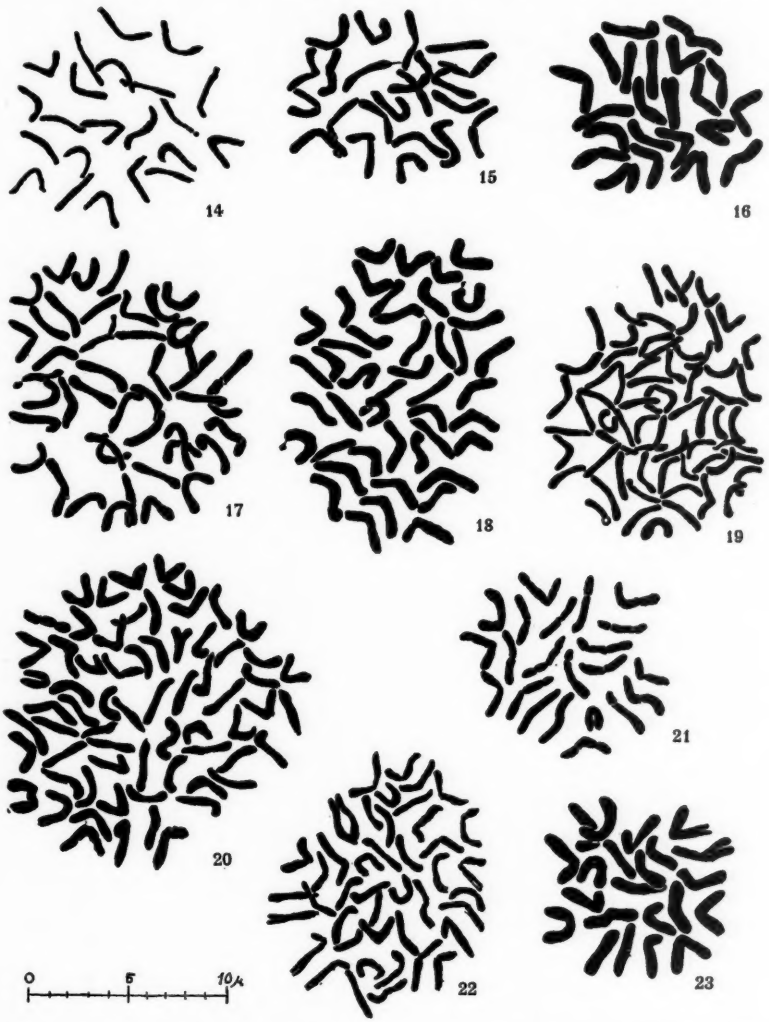

Fig. 14. *Asperula asperrima.* — Fig. 15. *A. taurina.* — Fig. 16. Diploides *Galium Mollugo.* — Fig. 17. Tetraploides *G. Mollugo.* — Fig. 18. Hypertetraploides *G. Mollugo.* — Fig. 19. Hexaploides *G. Mollugo.* — Fig. 20. *G. Schultesii.* — Fig. 21. Diploides *G. verum.* — Fig. 22. *G. laevigatum.* — Fig. 23. Diploides *G. lucidum.*

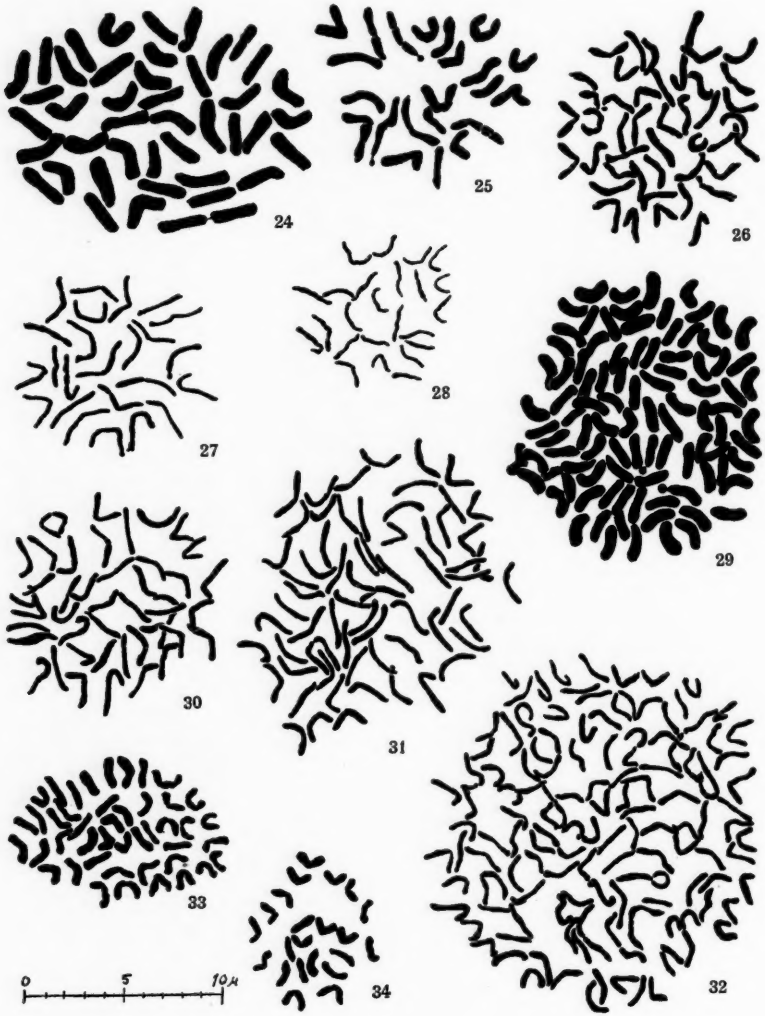

Fig. 24. *Galium ruthenicum.* — Fig. 25. *G. purpureum.* — Fig. 26. *G. saxatile.* — Fig. 27. Diploides *G. palustre.* — Fig. 28. *G. trifidum.* — Fig. 29. Octoploides *G. palustre* (Metaphase mit stark geschwollenen Chromosomen). — Fig. 30. Tetraploides *G. boreale.* — Fig. 31. *G. physocarpum.* — Fig. 32. *G. rubioides.* — Fig. 33. *G. vernum.* — Fig. 34. *G. cruciata.*

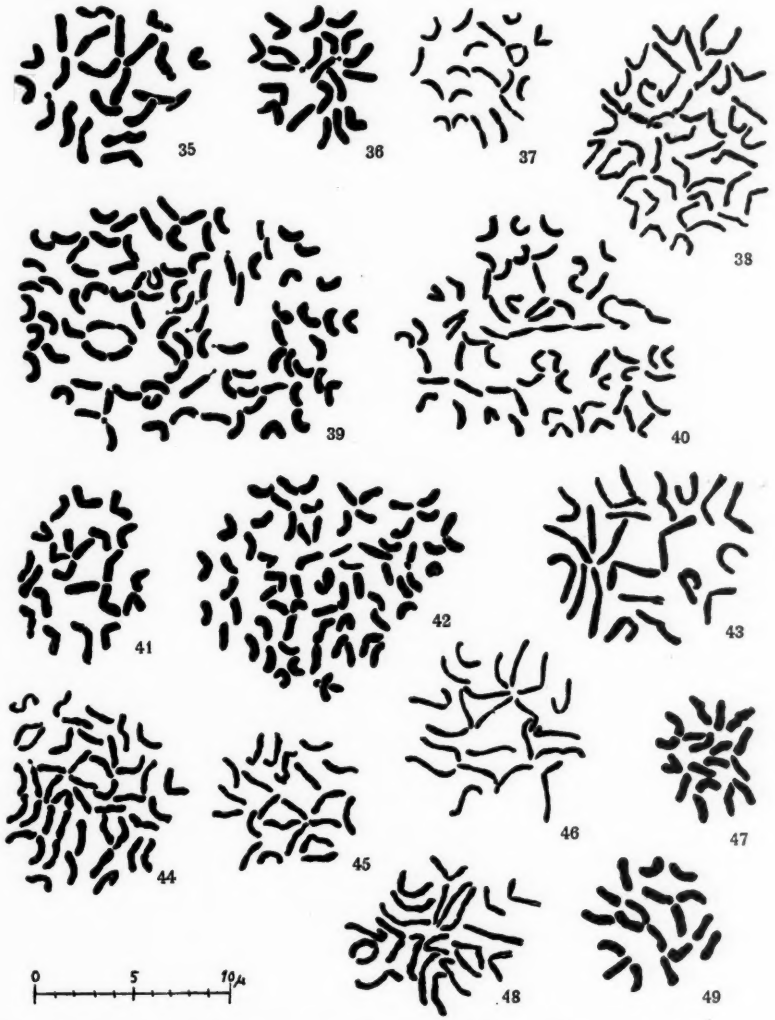

Fig. 35. *Galium saccharatum.* — Fig. 36. *G. Vaillantii.* — Fig. 37. *G. spurium.* — Fig. 38. *G.* sp. vom Richthofengebirge. — Fig. 39. Octoploides *G. aparine.* — Fig. 40. Hexaploides *G. aparine.* — Fig. 41. Diploides *G. parisiense.* — Fig. 42. Hexaploides *G. parisiense.* — Fig. 43. *Mericarpaea vaillantoides.* — Fig. 44. Tetraploides *G. setaceum.* — Fig. 45. Diploides *G. setaceum.* — Fig. 46. *G. cassium.* — Fig. 47. *Vaillantia muralis.* — Fig. 48. *Callipeltis cucullaria.* — Fig. 49. *Vaillantia hispida.*

diploiden oder aus einer hexaploiden herzuleiten muss angenommen werden, dass es in der *aparine*-Serie auch diploide und tetraploide und in der *palustre*-Serie tetraploide (und hexaploide?) Arten gibt. Desweiteren gibt es vermutlich, wenn auch theoretisch nicht unbedingt notwendig, ein diploides *Galium boreale*. In der Gattung *Asperula* können *A. montana* und *A. Neilreichii* als »Formen» von *A. cynanchica* betrachtet werden und dies haben auch mehrere Systematiker getan; ausserdem kann möglicherweise *A. asperrima* als eine »Form» von *A. glauca* aufgefasst werden. Es sollte also in der Gattung *Asperula* zwei ähnliche Serien geben. Dass die Serien nach oben durch die Zahlen 44, 66 oder 88 (96) abgeschlossen sind, braucht nicht der Fall zu sein, auch braucht nicht angenommen zu werden, dass die polyploiden Serien jeder einzelnen Art der *Stellatae* mit den neun (elf?) bis jetzt gefundenen abgeschlossen sind. In der Gattung *Galium* (*Stellata*-Gruppe) macht sich also eine ausgeprägte Neigung zur Erhöhung der Chromosomenzahl innerhalb einer und derselben Art bemerkbar, eine Neigung, die bei keiner anderen Pflanzengattung beobachtet worden ist. Es ist möglich, dass es auch unter den übrigen Rubiaceen ähnliche Serien gibt. Repräsentiert vielleicht *Coffea* eine solche?

Vorstehend ist angenommen worden, dass eine Art von sowohl Diploiden wie Polyploiden repräsentiert wird, mit anderen Worten, dass Autopolyploidie vorliegen soll. Ist das aber wirklich der Fall oder haben wir es mit Allopolyploiden zu tun, die durch Verdoppelung der Chromosomen bei Bastarden zwischen einander nahestehenden aber doch verschiedenen Arten entstanden sind? Bezüglich der drei ersten Serien muss man unbedingt antworten, dass hier Autopolyploidie vorliegt. In jeder einzelnen Serie sind nämlich die Polyploiden einander verblüffend ähnlich. Die hochpolyploiden sind hier durch Verdoppelung der Chromosomenzahl bei Arten mit geringer Variationsbreite entstanden. Die Glieder der sechsten bis neunten Serie variieren sehr stark, aber schon auf Grund der Autopolyploidie in den ersten Serien können wir vermuten, dass auch die letzteren durch Autopolyploide repräsentiert werden. Ausserdem stimmen die Aufteilungen in »Klein-Arten», die von Systematikern gemacht worden sind, nicht mit den Chromosomenzahlen überein. Wählt man z. B. *G. Mollugo*, so ist diese Linneanische Art etliche Male in mehrere »Arten» aufgeteilt worden. Die Aufteilung in die Arten *G. Mollugo*, *elatum* und *erectum* dürfte die gebräuchlichste sein. Es gibt aber sowohl ein diploides wie ein tetraploides »*G. elatum*»; von »*G. Mollugo* im engeren Sinne» gibt es Diploide, Tetraploide und Hexaploide und von »*G. erectum*» wenigstens

Tetraploide und Hexaploide. Die letzteren Serie dürfte man sich also aus Autopolyploiden von Arten mit grosser Variationsbreite zusammengesetzt denken können. Die Annahme von Autopolyploidie bei der *Stellatae* erhält dadurch eine Stütze, dass während der Reduktionsteilung Multivalente, wenn auch in geringer Anzahl, auftreten. DARLINGTON und andere haben gefunden, dass Autopolyploide im Vergleich mit ihren diploiden Stammformen eine herabgesetzte Fertilität haben. Bei den *Galium*-Serien ist das nicht der Fall, was wohl von der niedrigen Multivalenthäufigkeit abhängig sein dürfte. Kreuzungsversuche, leider in zu kleinem Umfange ausgeführt um ein sicheres Resultat zu erzielen,

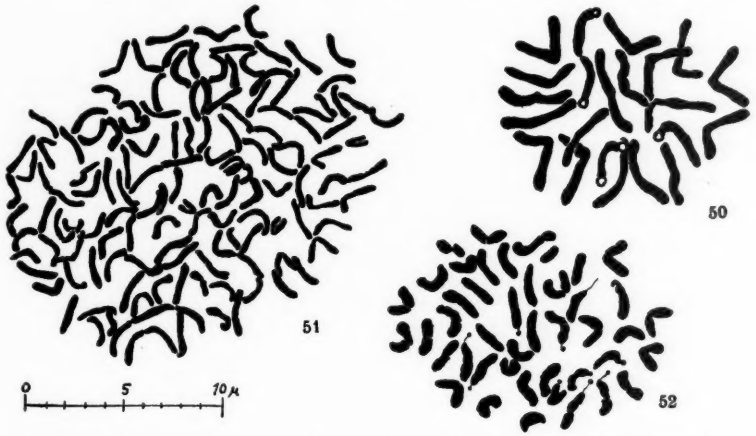

Fig. 50. *Rubia cordifolia.* — Fig. 51. *R. peregrina.* — Fig. 52. *R. tinctoria.*

deuten darauf hin, dass die verschiedenen Polyploiden des *G. Mollugo* »incompatibel» sind. Die Versuche werden fortgesetzt.

In einer solchen Pflanzengattung wie *Galium*, wo der Einschlag von Autopolyploiden gross ist, kann das Entstehen von neuen allopolyploiden Arten in einer Weise gedacht werden, die meines Wissens von Zytologen und Genetikern nicht beachtet worden ist.

Bezeichnet man den Chromosomensatz des diploiden *G. Mollugo* mit *MM*, so wird der des entsprechenden Autotetraploids *MMMM*, des diploiden *G. verum* mit *VV*, so wird der des entsprechenden Autotetraploids *VVVV*. Kreuzt man die diploiden Typen, erhält man den Bastarden *MV*, der natürlich in F_2 aufspalten wird (wenn F_1 fertil ist). Wenn jetzt aus irgendeiner Ursache eine Verdoppelung stattfindet, erhält man die neue allotetraploide Art *MMVV*; dieselbe erhält man aber

schon in F_1, wenn man die tetraploiden Typen kreuzt. Demnach sollte also der Bastard zwischen den tetraploiden *G. Mollugo* und *G. verum* konstant werden und sich ganz wie eine Art verhalten. Allotetraploide Arten können also in F_1 durch Kreuzung zweier Autotetraploiden entstehen. Die Hybride *Galium Mollugo* × *verum* ist mit einem eigenen Artnamen (*G. ochroleucum* WOLFN., *G. decolorans* GREN.) belegt worden. Die Art hat, wie ich selbst gesehen habe, guten Pollen und gute Samenbildung. HOMEYER gibt an, dass sie vollkommen normale Reduktionsteilung hat und bezüglich der Keimkraft des Pollens und der Samen den Eltern nicht nachsteht. Die Zukunft wird zeigen, ob wir hier wirklich eine neue allotetraploide Art vor uns haben; würde dies der Fall sein, so ist zugleich die Autopolyploidie in der Gattung *Galium* vollkommen bewiesen.

Kreuzungsversuche, die in kleinerem Umfange schon mit *G. Mollugo* und *verum* begonnen worden sind, dürften auch zur Lösung der Frage nach der vermuteten Entstehungsart der Autopolyploiden führen.

Botanisches Institut der Hochschule zu Stockholm im November 1933.

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ON THE ORIGIN AND PRESERVATION OF POLYPLOIDY

BY *OTTO HEILBORN*

STOCKHOLM

I. INTRODUCTION.

POLYPLOIDY, or the occurrence of multiple chromosome sets in organisms, is now a well-established fact in the vegetable kingdom. However, the frequency of this phenomenon is very different in the various families or groups of plants. Among animals polyploidy is almost absent. These peculiar differences between the various groups of organisms required some explanation, and, in fact, since 1925 quite a series of such explanations have been put forward by various authors. There has also been some controversy as to the validity of the different opinions. To the present writer the controversies do not, however, appear fully justified, and this for the following reason. Some of the hypotheses deal, principally, with the *origin* of polyploidy, others, again, with the *preservation* of such polyploidy as has already arisen. Some deal mostly with *animals*, others with *plants*. A hypothesis dealing with one phase of the phenomenon does not necessarily exclude other interpretations that deal with other phases. In the following the various hypotheses on the occurrence or absence of polyploidy are being discussed from the last-mentioned point of view.

With regard to their *ancestry*, polyploids may be divided into two classes: *autopolyploids* and *allopolyploids* (KIHARA and ONO 1926). Also with regard to the *mechanism of origin*, polyploids may be divided into two classes: those due to *somatic doubling* (inclusive doubling in the fertilized egg and doubling in pre-meiotic divisions), and those owing to *failure of reduction* in gametogenesis. There is, perhaps, also the possibility of dispermic fertilization. For details the reader is referred to the recent works by DARLINGTON (1932), SANSOME and PHILP (1932), WINGE (1932) and HEILBORN (1932 b).

II. THE HYPOTHESES.

The various hypotheses dealing with the differences in frequency of polyploidy in different groups of organisms shall now be briefly considered, partly in chronological order.

First hypothesis. MULLER (1925) advanced the idea that *the sex-chromosome mechanism might be the cause of the almost total absence of polyploidy among animals.* The sex-chromosome mechanism is assumed to act, chiefly, in two ways. A normal proportion between x-chromosome and autosomes is assumed to be a conditio sine qua non for a regular development of sex, and thus for sexual reproduction. This normal development is disturbed in triploids, hexaploids etc. where the ratio of x to autosomes has been changed. In tetraploids and octoploids, on the other hand, the ratio of x to autosomes is retained unchanged, and sex-development is normal. Tetraploids and octoploids, however, suffer from a second influence of the sex-chromosome mechanism: though they themselves are normally developed, all male sex-organs (in *xxyy* males and similar types) produce a great proportion of gametes with an abnormal equipment of sex-chromosomes. This is assumed to decrease the capacity of sexual reproduction in tetraploids and octoploids.

According to this theory, the most important effect of the sex-chromosome mechanism appears to be *the elimination of all such polyploids as develop into sterile hermaphrodites or intersexes.* When polyploidy leads to hermaphroditism, it exercises thus a destructive effect on most animals, perhaps also on many liverworts (HEITZ 1927), but generally not on higher plants.

It is a very noteworthy fact that parthenogenesis is characteristic of most of the few polyploid animals known in a natural state. This is quite in accord with MULLER's explanation. Parthenogenesis has obviously facilitated the survival of these animals.

Dioecism in polyploid plants may be of secondary origin, and does not constitute a reason for disproving MULLER's hypothesis.

Second hypothesis. As a separate hypothesis may be regarded the brief statement by FEDERLEY (1932 a, p. 14) to the effect that the lack of polyploidy among animals may probably be due to *the extreme rarity of self-fertilization* — even among normally hermaphrodite animals. This rarity of self-fertilization probably acts in several ways. If unreduced gametes are formed, the fusion of two such gametes is made very improbable by the prevention of self-fertilization: hence, the origin of tetraploids is made difficult. If, on the other hand, tetraploids are once formed, they have generally originated as *single* individuals and are, then, inevitably, fertilized by diploids: hence their offspring consists mostly of triploids, and the tetraploids are unable to maintain themselves.

The prevention of self-fertilization may be brought about not only by lack of hermaphroditism but also by the structure of the sex-organs, or by factors of incompatibility. It is not directly owing to the balance of sex-chromosomes.

Third hypothesis. The great importance of *cell-constancy or eutely* for the different frequency of polyploidy among animals and plants was first emphasized by WETTSTEIN (1927, p. 328), and has later been more fully discussed by the present writer (HEILBORN 1933). Eutely is regarded as the outcome of an equilibrium in tissues and organs, arising from the co-operation of cell and nuclear sizes with rates of cell-division and organ-sizes. In animals, these factors co-operate in such a way as to establish a high degree of constancy of cell-numbers in the various organs. In plants, again, this cell-constancy is, generally, much less pronounced, and a regulatory change in cell-number may be achieved comparatively easily.

In organisms with a very decided cell-constancy a doubling of the chromosome number and a corresponding increase in nuclear size and cell-size is bound to lead to a heavy increase in organ-size and often to abnormal development. WETTSTEIN's researches on mosses indicate that this has probably a lethal effect on many polyploids. This may account for a more or less complete *extermination of polyploids among animals* (*where eutely is strong*). Further researches into cell-constancy seem desirable.

Fourth hypothesis. NEWTON and PELLEW (1929, p. 412) suggest the following explanation. »It does not appear that somatic doubling is more common in hybrids than in pure-bred plants. It is possible that a reason for the greater commonness of polyploid series in plants than in animals is that, owing to their different mode of growth, such »mutated cells» are more likely to give rise ultimately to germ cells».

According to this hypothesis somatic doubling might take place among animals about as often as among plants but the effect upon the animal germ-cells is supposed to be small. Hence, *the origin of polyploidy by means of somatic doubling is rare among animals.* The hypothesis relates to somatic doubling only (not to failure of reduction) and does not, therefore, account for more than a minor part of the differences between plants and animals.

Fifth hypothesis. According to ARTOM (1928, cited by CHIARUGI 1933, p. 15) autopolyploidy is the only form of polyploidy found among animals. The cases found are rare. One might suggest that these cases may be the results of somatic doubling; the scarcity of the phe-

nomenon is then in consonance with the hypothesis of NEWTON and PELLEW.

The possible connection between somatic doubling and autopolyploidy may be explained in about the following way. Somatic doubling as a rule seems to occur with about the same frequency in hybrids as in pure species. *Under natural conditions, however, individuals of pure species are far more numerous than those belonging to hybrids.* A process of somatic doubling, *operating by chance*, must, therefore, be assumed to give rise — still under natural conditions — to a certain number of autopolyploids but only rarely to allopolyploids. According to all our experience from plant hybrids the production of unreduced gametes is, on the other hand, a special characteristic of hybrids and a comparatively rare event in pure species. The formation of polyploid offspring through the failure of reduction is thus not a process operating by chance. On the contrary, it operates chiefly in hybrids, and gives rise to allopolyploids. The conclusion is obvious: *if a group of organisms shows a certain degree of autopolyploidy, but no allopolyploidy, the polyploids must be assumed to have originated by somatic doubling.*

There is still another reason for regarding the few animal polyploids as the outcome of somatic doubling. It is a widely accepted view among botanists that parthenogenesis or apogamy among plants is especially common among hybrids. If the same holds good for animals, and if parthenogenesis is especially frequent in polyploids (conf. above), one must expect polyploid animals to be, preponderatingly, allopolyploids. This is not the case.

With regard to *Lepidoptera*, many interesting details are to be found in a recent summary by FEDERLEY (1932 b). »Bei den Lepidopteren werden wohl, soweit die Verhältnisse bis jetzt bekannt sind, die diploiden Gameten nicht die Möglichkeit haben, neue Arten zu bilden, sie sind schon bei ihrer Bildung dem Untergange geweiht« (p. 377). »Denn wenn es auch bekannt ist, dass viele Bastarde Spermien bilden, die tatsächlich einen vollständigen Chromosomensatz beider Eltern enthalten, so ist bis jetzt kein einziges solches Ei gefunden worden« (p. 376).

We conclude: polyploidy hitherto known among animals is autopolyploidy, probably occasioned by somatic doubling; animal polyploidy as a rule does not occur through failure of reduction; animal allopolyploidy is as yet unknown. *The extreme rareness of animal polyploidy might thus be caused by the rareness, or lack of survival, of*

unreduced gametes in normally sexual animals. This is our fifth hypothesis.

GATES (1929, cited according to MÜNTZING 1933, p. 53) appears to support similar ideas. It is not improbable that the production of unreduced gametes is, for some reason, rendered difficult among animals. It may especially be questioned whether the maturation of the animal egg, with extrusion of polar bodies, can be changed in such a way as to give rise to restitution nuclei (ROSENBERG 1926—27).

With regard to higher plants, one may ask in a similar way which type of embryo-sac is most likely to develop restitution nuclei, the »normal» embryo-sac originated from a single tetrad cell, or the embryo-sac of »*Lilium*-type» into which all four cells of the megaspore tetrad merge. Nothing is as yet known on this subject. Experiments with low temperatures might contribute to the elucidation of the problem.

Sixth hypothesis. The writer has found the following cytological conditions in the genus *Carex* (HEILBORN 1932 a, p. 142 f.). »About 70 species and forms have now been investigated — —, and all but one (*C. glauca*) lack every trace of polyploidy». This species is shown to be autotetraploid. »It seems safe to conclude that within the genus *Carex* aneuploidy is prevalent, while allo-polyploidy is lacking, and auto-polyploidy has so far been found in only one exceptional case». The autotetraploid *Carex glauca* is supposed to have originated through somatic doubling. — It should be added that HÅKANSSON (1929) has found two races of *Scirpus palustris*, one with 19 chromosomes (haploid) and one with 8. The former appears to be a derivated autotetraploid. No further cases of polyploidy have been met with in the family *Cyperaceae.*

The writer (l. c.) has tried to explain the peculiar lack of allopolyploidy in this family with a reference to its likewise very peculiar pollen formation. Of the pollen tetrads always three cells degenerate and die, while only the fourth survives. »There is obviously a tendency, of an unknown nature, for three quarters of a pollen tetrad to degenerate, and this inherent tendency probably prevents the formation of unreduced pollen dyads in species hybrids» (l. c. p. 144). *Hence, such polyploidy as is occasioned by the production of unreduced gametes is lacking.* As unreduced gametes are, generally, not formed in pure species but, preponderatingly, in species hybrids, *a lack of allopolyploidy will result.* It will be seen that this hypothesis does not differ materially from the preceding »fifth hypothesis».

MÜNTZING (1933, p. 51) has argued against this explanation. There

are, mainly, two objections: 1) »that unreduced female gametes may be formed which would suffice to produce allotetraploids»; 2) that »allopolyploids just as well as autopolyploids might arise by somatic doubling».

MÜNTZING's objections do not, however, pay due regard to the *frequency* of polyploidy arising in different ways. If doubling of the chromosome number through failure of reduction occurs in the female gametes only, polyploidy arising in this way probably becomes relatively rare, while doubling in both sexes must result in much more frequent polyploidy. The rarity of polyploidy in *Cyperaceae* is thus in good consonance with the writer's hypothesis. The same holds good as regards MÜNTZING's second objection. According to the aforesaid considerations somatic doubling must be assumed to give rise, preponderatingly, to autopolyploids. If in *Carex* 1 autopolyploid has arisen, through somatic doubling, among 70 species there is, perhaps, but 1 allopolyploid to be found among 700 species. The chance of finding this allopolyploid is very small. It has not yet been found, though the possibility of its existence cannot be denied. The writer's hypothesis is thus still in good accord with chromosome conditions in *Cyperaceae*.

On the other hand, the application of MÜNTZING's hypothesis of double fertilization (conf. below) meets with difficulties. MÜNTZING's own conclusion is guarded: »Thus, as far as the evidence goes the conditions in *Carex* are not in opposition to the theory that double fertilization and polyploidy in Angiosperms are causally connected». This may be true but it is nevertheless impossible to explain the lack of polyploidy in *Carex* with the aid of this theory. For an explanation MÜNTZING himself resorts to auxiliary hypotheses.

Seventh hypothesis. MÜNTZING (l. c.) refers in this connection to the possibility of chromosome fragmentation through which original polyploidy might have been obscured and levelled. Chromosome fragmentation was suggested already by the present writer (1924) as a possible explanation in *Carex*, and this suggestion has later, to a certain extent, been confirmed by LEVAN (1932, p. 276).

On the whole it may be assumed that *groups of organisms with abundant chromosome fragmentation will show much aneuploidy* (or, rather, disploidy according to CHIARUGI, l. c.) and little polyploidy.

Eighth hypothesis. Another suggestion has been made by MEURMAN (1929, p. 93). According to him aneuploidy in *Carex* might have arisen as a result of irregular meiosis in autopolyploids. This explanation is scarcely in good accord with facts. The single autopolyploid hitherto

found in *Carex* appears to have a very regular meiosis, and autopolyploidy seems, on the whole, to be far too rare in this genus to account for the very frequent aneuploidy (or disploidy). On the other hand, MEURMAN's explanation agrees with the writer's in assuming allopolyploidy to be rare, or absent.

As a rule it may be assumed that *groups of organisms showing autopolyploidy, but little tendency to allopolyploidy, will exhibit aneuploidy.* »In families on the other hand where the serial arrangement of the chromosome numbers is clear and the chromosome numbers constant, a strongly allopolyploid condition seems to be indicated» (MEURMAN, l. c.).

Ninth hypothesis. H. J. SAX (1932) studied the chiasma formation of chromosomes in some Conifers and found the terminalization of chiasmata during meiotic prophase to be small. At the same time the average number of (mostly interstitial) chiasmata per bivalent was regarded as relatively high (about 2,1 in two *Larix*-species and one hybrid investigated). From this the conclusion is drawn that »any autopolyploids produced would be expected to form closely paired tetravalents. The segregation of homologous chromosomes in such polyploids would probably be too irregular to produce a high degree of fertility, and the polyploid would have small chance of survival». This is supposed to explain, partly at least, the rarity of polyploidy in Conifers.

SAX's hypothesis refers solely to autopolyploidy and does not explain the lack of allopolyploidy among Conifers. As allopolyploidy is by far the commoner type among plants — at least under natural conditions — the hypothesis has no wide scope. Besides, it has no solid foundation in cytological facts. DARK (1932) found a vigorous terminalization in *Taxus baccata* and a decided reduction of interstitial chiasmata. The average chiasma frequency per bivalent in *Taxus* is about 2 and this is regarded as a quite ordinary frequency. The chromosome behaviour in Gymnosperms is said to be similar to that described in Angiosperms. On the whole there seems, therefore, to be little reason to seek the cause of the differences in the frequency of polyploidy in chiasma formation. H. J. SAX's hypothesis presents, as is easily noted, a certain resemblance to MEURMAN's.

Tenth hypothesis. This is the explanation given by MÜNTZING (1930, 1933). According to him the *double fertilization and endospermic development in Angiosperms leads to a regular chromosomal balance* between embryo, endosperm and the surrounding tissue. *If this balance*

is disturbed, e. g. through crossing, there are serious effects upon the offspring. There will be especially a high mortality among the young embryos. In this way *aneuploid offspring is exterminated*, while diploid and polyploid plants survive. Among animals, again, the endospermic mechanism is lacking. MÜNTZING regards this circumstance as »a main cause of the characteristic difference in frequency of polyploidy between animals and higher plants» (1933, p. 53).

In the writer's opinion, however, MÜNTZING has somewhat overestimated the scope of his theory. His explanation accounts pretty well for the rarity of aneuploidy among higher plants, but probably not for the rarity of polyploidy, particularly not the absence of allopolyploidy, among animals. It accounts nicely for the relative frequency of aneuploidy in *Orchidaceae*, where endospermic development is absent or feeble; but it does not account for the remarkable stability of the chromosome set in Conifers where double fertilization is lacking. In the latter case one might just as well have expected to encounter numerous polyploid and aneuploid types; the stability in Conifers is no proof of MÜNTZING's hypothesis.

In his paper of 1930 (p. 169) MÜNTZING criticises MULLER, but in the opinion of the present writer the two theories do not contradict one another. MÜNTZING's hypothesis tries to explain the *elimination of aneuploidy among higher plants*; MULLER's the *elimination of polyploidy among animals*. They do not preclude one another.

Eleventh hypothesis. The doubling of the chromosome number generally leads to an increase in nuclear size and cell-size, and then often to gigantism. This may have an injurious effect on the polyploids. If special genes or gene-combinations exist which counteract these effects of nuclear enlargement, polyploids may escape injury and survive. DARLINGTON (1932, p. 207) thinks that »the failure of polyploidy to appear in many groups of flowering plants may be due to failure of such species to segregate or mutate to dwarfness». The genes for »dwarfness» might be imagined as affecting all kinds of relations between chromosome number and phenotypic expression of size, even cell-size. Though this explanation may be true, there is little positive evidence in its favour.

Twelfth hypothesis. DARLINGTON (1932) has furthermore suggested that *the chromosomes in some plant groups are too long to permit of a regular behaviour* of the nuclei in a polyploid condition. Polyploid nuclei are supposed to be unable to behave normally, especially in

meiosis, when the chromosome length becomes excessive. This would explain the rarity, inter alia, of polyploidy in many genera of *Liliaceae*.

III. CONCLUDING REMARKS.

As will be seen from the preceding account, there is a great diversity of opinion, and it is almost impossible to estimate properly the validity of the various views. The writer will, therefore, confine the following discussion to a few additional remarks.

The following hypotheses deal with *the rarity of polyploidy among animals*: Nos. 1, 2, 3 (chiefly at least), 4 and partly 5 and 7. No. 10 deals with *the rarity of aneuploidy among Angiosperms*. Nos. 6, 8, 9, 11, 12 and partly 5 and 7 deal with *the rarity of polyploidy within certain groups of higher plants*.

The following hypotheses are closely connected with the problem of the *origin* of polyploids by means of somatic doubling or unreduced gametes and the survival of the young embryos and larvae: Nos. 2 (partly), 3, 4, 5, 6, 10 (partly) and 11. The following, again, deal, principally, with the *preservation* of such polyploids as have reached the adult stage: Nos. 1, 2 (partly), 7, 8, 9, 10 (partly) and 12.

A prolific development of polyploidy, such as is found in many Angiosperm families, obviously requires a certain amount of co-operation of several simultaneous circumstances: 1) the occurrence of somatic doubling or the production of unreduced gametes; 2) only a slight degree of cell-constancy; 3) possibilities for self-fertilization; 4) capacity of enduring a change from separate sexes to hermaphroditism; 5) double fertilization, parthenogenesis or other incompatibility barriers which prevent the swamping of the newly established polyploids by crossing with the diploid parents; 6) favourable chromosome conditions that enable a regular meiosis in the polyploids. If one or more of these conditions fails, polyploidy becomes rare or maybe altogether lacking.

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